AN INTRODUCTION TO SEXUAL PHYSIOLOGY

AN INTRODUCTION TO SEXUAL PHYSIOLOGY

For Biological, Medical, and Agricultural Students

BY

F. H. A. MARSHALL, F.R.S.

AUTHOR OF "THE PHYSIOLOGY OF REPRODUCTION"

WITH ILLUSTRATIONS

LONGMANS, GREEN, AND CO.

55 FIFTH AVENUE, NEW YORK

39 PATERNOSTER ROW, LONDON

TORONTO, BOMBAY, CALCUTTA, AND MADRAS

1925

Made in Great Britain.

PREFACE

In preparing this little book I have been actuated by the desire to supply those who are interested with a concise account of the more important sexual and reproductive processes in the higher animals and man. Although it is called "An Introduction," the subject is dealt with much more fully than is done in any ordinary text-book treating of the whole of physiology. Readers who require a more extensive knowledge may be referred to my larger work on "The Physiology of Reproduction," and to Professor Lipschütz's book on "The Internal Secretions of the Sex Glands." The present work is intended primarily for biological, medical, and agricultural students, but it is hoped that it may be of use also to others who possess only a rudimentary knowledge of zoology or physiology. Indeed, had I not received repeated requests to write such a book as this aims at being, I should hardly have made the attempt.

My thanks are due to Dr A. S. Parkes who has very kindly read the section on the Determination of Sex, and given me the benefit of his helpful criticism. I am likewise indebted to Mr J. T. Saunders who has looked through the chapter on Pregnancy. I wish to thank Mr J. H. Bullock for the care he has taken in the preparation of the index and in the final revision of the proofs. I am under obligations also to all those authors and publishers who have kindly allowed me to reproduce illustrations from the respective works belonging to them.

The subject of the book is one which is rapidly advancing, and I have taken the opportunity of including in it some account of investigations which have been published since the last edition of my larger work was issued. The present work may therefore be regarded as to some extent also a supplement to my former

book, although, in conformity with the general plan, I have kept the subject-matter as elementary as possible. Moreover, I have included in it certain matters, such as a description of the development of the embryo and a short account of the phenomena of hereditary transmission, which are not found in "The Physiology of Reproduction."

Lastly, I make no apology for concluding the work with a reference to the birth-rate in man and the problem of human population. My final paragraph is quoted from an article by Mr J. M. Keynes, published in a special supplement to *The Manchester Guardian*, and dealing with "Reconstruction in Europe" (No. VI., 1922); to this the reader is referred for much detailed information, as well as for the views of a symposium of thinkers, concerning the post-war position of a problem, the biological interest of which is only surpassed by its supreme social importance.

F. H. A. MARSHALL.

CHRIST'S COLLEGE,
CAMBRIDGE, 25*th March*, 1925.

CONTENTS

CHAPTER VI.

CHAPTER VII.

CHAPTER VIII.

LIST OF ILLUSTRATIONS

AN INTRODUCTION TO SEXUAL PHYSIOLOGY

CHAPTER I

INTRODUCTORY

As is well known to every student of biology, all living organisms, both vegetable and animal, consist of one or more cells. Each cell is composed of protoplasm which is the physical basis of all life. and the vital substance forming the most highly developed animals differs in degree rather than in kind from the undifferentiated protoplasmic mass comprising the most simple form of life known. Protoplasm itself is a semi-fluid, transparent, viscous substance made up chiefly of nitrogenous compounds or proteins, but containing also small quantities of fats and carbohydrates together with sulphur and phosphorus in a combined form, as well as certain metals. It is generally enclosed by a membrane which consists of the outer layer of the cell, and within it is a small, round specialised body known as the nucleus, which can usually be easily identified under the microscope by its more intense staining capacity. The nucleus is essential to the life of the cell.

The simplest forms of animals and plants are unicellular, and of these the amœba, a microscopic organism found in pond water, is a well-known example. In this animal all the vital functions of the body are discharged by one cell which may be seen to move spontaneously by protruding a part of its substance, to eat up small particles of food by permitting a portion of its protoplasmic contents simply to flow round them, to excrete waste products, to increase in size, and, finally, at a certain stage of its life history, to reproduce by a process of dividing into two. This is the simplest mode of generation found in any organism and

it is characteristic of the Protozoa among animals and the Protophyta among plants, where the entire substance of the body consists of a single undifferentiated cell. The nucleus undergoes division as well as the external protoplasm or cytoplasm outside the nucleus, so that each product of cell division comes to contain a nucleus just like the parent cell.

The higher forms of life consist of many cells, whole groups of which are separated off to subserve particular functions, and

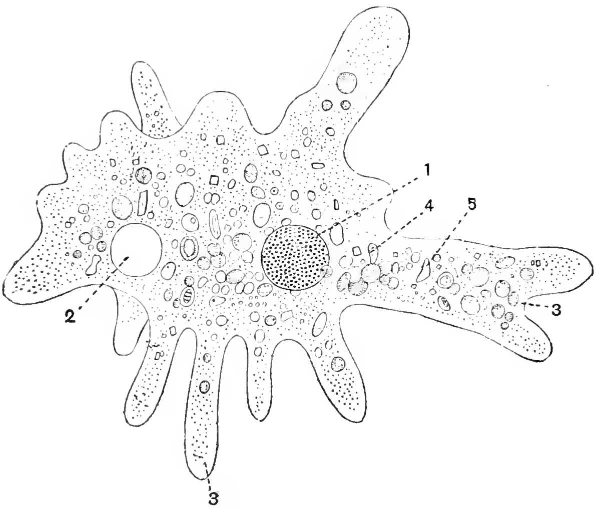


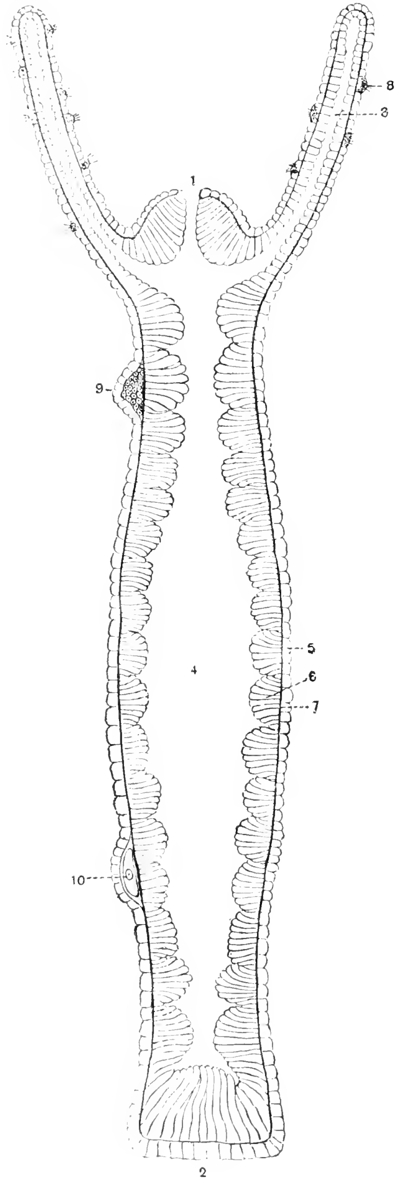
FIG. 1.—*Amœba proteus.* ×330. (After Gruber, from Shipley and MacBride's *Zoology*, Cambridge University Press.)

1, Nucleus; 2, contractile vacuole through which waste matter is excreted in solution; 3, pseudopodium; 4, food vacuole; 5, grains of sand.

these groups are packed together in various ways to form the different tissues. The body of a higher animal is, however, derived from a single cell, and this in the process of individual development undergoes a long series of divisions in the course of which the nuclei also divide. The products of division, that is to say, the cells with their contained nuclei, become gradually specialised and so give rise to the tissues of various kinds—bone, cartilage, muscle, nerve, skin, gland, etc. Thus the outer layer becomes adapted for protection and for the reception of impressions produced by changes in the surroundings; the inner

layer lining the gut becomes concerned with the digestion and absorption of the food; while between these the skeleton and general framework of the body are developed, besides all the other organs and tissues which contribute to the performance of the vital functions. Amongst these are the generative organs or gonads which differ according to sex, male animals having testes and female ones ovaries, in which the actual reproductive cells, or spermatozoa and ova, are respectively produced. Thus in the bodies of the higher animals—and the same is true of the higher plants—certain specialised cells are produced, the function of which is to unite and to reproduce. In the process of fusion as it occurs in all multicellular animals a single spermatozoon unites with a single ovum, the two nuclei also uniting, and this fusion of the generative cells or gametes to form one cell, known as the zygote, is the essential act in sexual reproduction.

Asexual Reproduction.—As we have seen already in unicellular organisms like the amœba reproduction takes place by binary fission, without any further complicating process. This method is the simplest form of asexual reproduction. The two products of division go on growing until they have reached a certain size, and then they divide again, and so the process is repeated. In some multicellular animals also reproduction takes place by binary fission. Thus in the sea anemone the whole body occasionally divides into two equal portions, and the same is true for certain small flat worms when nutritive conditions are especially favourable. In such cases the products of division go on growing until they reach the size of the parent individuals. A much commoner mode of asexual reproduction among multicellular animals is that of budding or gemmation where the body divides unequally. The common fresh-water polyp or Hydra is a well-known example of an animal in which budding occurs. There is at first a pouch-like outgrowth of the body wall, and this is the starting-point of the new offspring. As the bud increases in size the characteristic tentacles and mouth of the young polyp make their appearance and the other organs and structures are gradually formed. Eventually the bud constricts at its base and breaks off from the parent, so becoming an independent individual which goes on growing till it reaches the size of the parent. Reproduction by budding is very common among the lower groups of the animal kingdom. The individuals produced in this way often remain



attached to the parent stem and form multiple individuals or colonies in the manner characteristic of sponges and corals. Among the higher plants also propagation may take place by budding as well as by the sexual method.

Allied to the process of budding is that of the regeneration of lost parts of the organism or of structures submitted to injury.

Fig. 2.—Longitudinal section through *Hydra*, magnified (diagrammatic).

(From Shipley and MacBride's *Zoology*, Cambridge University Press.) 1, Mouth; 2, foot; 3, tentacle; 4, digestive cavity; 5, ectoderm or outer layer of cells; 6, endoderm or inner layer; 7, intermediate structureless lamella; 8, batteries of thread cells used for killing prey; 9, testis; 10, ovary with ovum.

This power is possessed in some degree even by the higher animals, as with the limbs of a newt or salamander which grow again after being destroyed. Among some of the lower forms of life, however, complete individuals may be regenerated, as when a flat worm is divided into a number of pieces each of which can develop into a new individual.

Conjugation.—It has been mentioned that sexual reproduction

is characteristic of all the higher plants and higher animals, some of which, however, also reproduce asexually. It is important to note that even among unicellular organisms whose ordinary method of multiplication is simple binary fission there is sometimes a distinct process of a sexual kind consisting of the union of two individuals, and this process is known as conjugation. The union may be either permanent or temporary, and when it is temporary there is an interchange of nuclear material carried out during the process. In each case the act is usually followed sooner or later by fission.

There is general evidence that conjugation has a rejuvenating influence and that the individuals concerned are better fitted thereby to perpetuate the race, but the problem as to the precise signification of the process is still obscure. Maupas was the first to deal with the problem experimentally, and his observations upon the conditions under which conjugation took place in the infusorian, Stylonichia, have become classical, though his conclusions can no longer be accepted in their entirety. Maupas found that Stylonichia could go on giving rise to new individuals by simple binary fission without any conjugating process taking place for 215 generations, but that at this stage the individuals produced were debilitated and no longer possessed the normal power of acquiring nutrition, and, moreover, the capacity to divide was lost, so that the strain died out. If, however, individuals were allowed to conjugate with other unrelated ones of the same species before the stage of exhaustion was reached, or at any time up to the 130th division, they became rejuvenated and multiplication by binary fission could go on as before. After the stage of exhaustion or debilitation had been reached it was difficult or impossible to induce conjugation. From such experiments Maupas drew the conclusion that there is a limit to the capacity to reproduce asexually, that is, without the occurrence of conjugation, and that the latter process, whereby a fusion of protoplasm from two different individuals takes place, is essential for the rejuvenation of the race, which cannot otherwise be perpetuated indefinitely.

Subsequent investigators, however, have found that in certain Protozoa multiplication by binary fission may go on apparently quite indefinitely without the intervention of conjugation at all. Thus Calkins stated that with the slipper animalcule or

Paramœcium senile degeneration could be avoided by supplying the culture with beef extract, and various observers have found that some small alteration in the environment, such as the addition of a minute quantity of alcohol or even a slight change in the composition of the water, may prevent deterioration from setting in and so admit of the continuation of binary fission without resorting to conjugation. As we shall see later, there is some evidence that whereas continuous and close inbreeding among the higher animals may lead to general deterioration and sterility, these consequences may be obviated and a relatively infertile race rejuvenated by access to a new environment.

On the other hand, conjugation among the Protozoa does not seem to be necessarily associated with reproduction, and according to Enriqués, conjugation only takes place with *Colpoda steini* under certain peculiar environmental conditions (*e.g.* if the layer of the water is less than 2 millimetres in thickness), and it has been suggested that the utility of the process depends upon the power given thereby to withstand adverse circumstances. It would seem also that the only feature common to conjugation and fertilisation among the higher animals is biparental inheritance which usually implies variation. Amid adverse conditions of existence conjugation is often more apt to occur, and it is possible that among the new combinations of variations brought about as a result of the process, there are some which are better suited to the altered circumstances, and that the advantage gained in this way is an important factor in the survival of the race. (See below, p. 123.)

Sexual Reproduction among Multicellular Animals.—With the species of Protozoa above cited the two conjugating cells unite, and each may be said to fertilise the other through the exchange of nuclear or other protoplasmic material or as a result of permanent union which is preceded by binary fission. In other species, however, such as Vorticella or the common bell-animalcule, there are two sexual individuals, one of which is attached by a contractile stalk to a water weed, and another smaller individual which is free-swimming and bores its way into the larger stationary one in the act of conjugation. Here we have a distinct foreshadowing of the differentiation of sex cells, which is characteristic of all the Metazoa or multicellular animals. We find also dimorphic reproductive cells in Volvox which consists of a colony of cells

joined together to form a ball, some of these colonies producing ova and some spermatozoa; the latter differ from the ova in being smaller and free-swimming. In all the higher animals the differentiation of the sex cells or gametes is very marked. The spermatozoon is a very small microscopic organism (in man it is ·05 millimetre long or about $\frac{1}{500}$ of an inch); in most species it is formed of a compact head which is the nucleus of the cell and a long slender vibratile tail. The spermatozoon propels itself forward by the movements of the tail. There is generally also

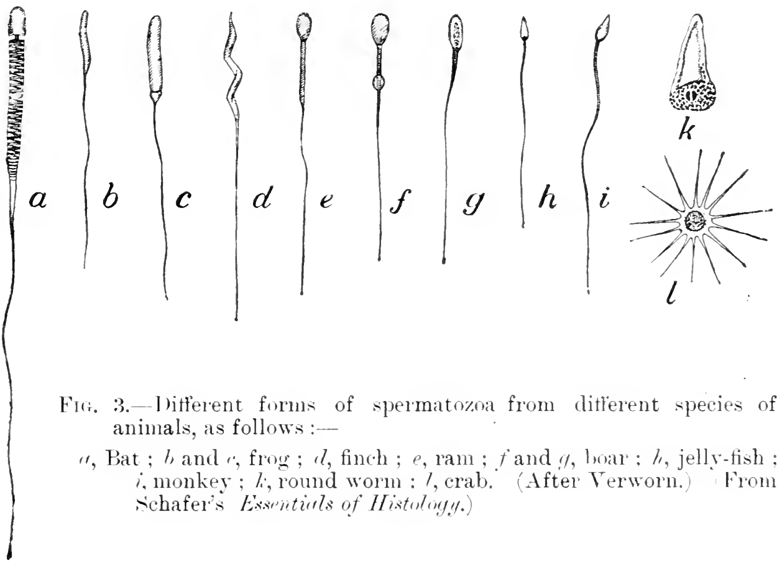


FIG. 3.—Different forms of spermatozoa from different species of animals, as follows:—

a, Bat; *b* and *c*, frog; *d*, finch; *e*, ram; *f* and *g*, boar; *h*, jelly-fish; *i*, monkey; *k*, round worm; *l*, crab. (After Verworn.) (From Schafer's *Essentials of Histology*.)

a more or less cylindrical middle piece between the head and the tail. The spermatozoon contains very little extra-nuclear protoplasm and therefore very little reserve food material. It is essentially adapted for locomotion, and it is by means of its active swimming movements that it comes into contact with the ovum which it fertilises. Ova or eggs, on the other hand, are inert bodies and contain food material, generally in the form of yolk and sometimes in very great quantity. They are almost invariably spherical. They vary in size according to the kind of animal, those of a mammal being microscopic, although much larger than the spermatozoa (the human ovum has a diameter of ·2 millimetre

or about $\frac{1}{125}$ of an inch), while there are all gradations up to the egg of the ostrich which is more than 3 inches in length, and that of the Japanese shark which is over 8 inches. In

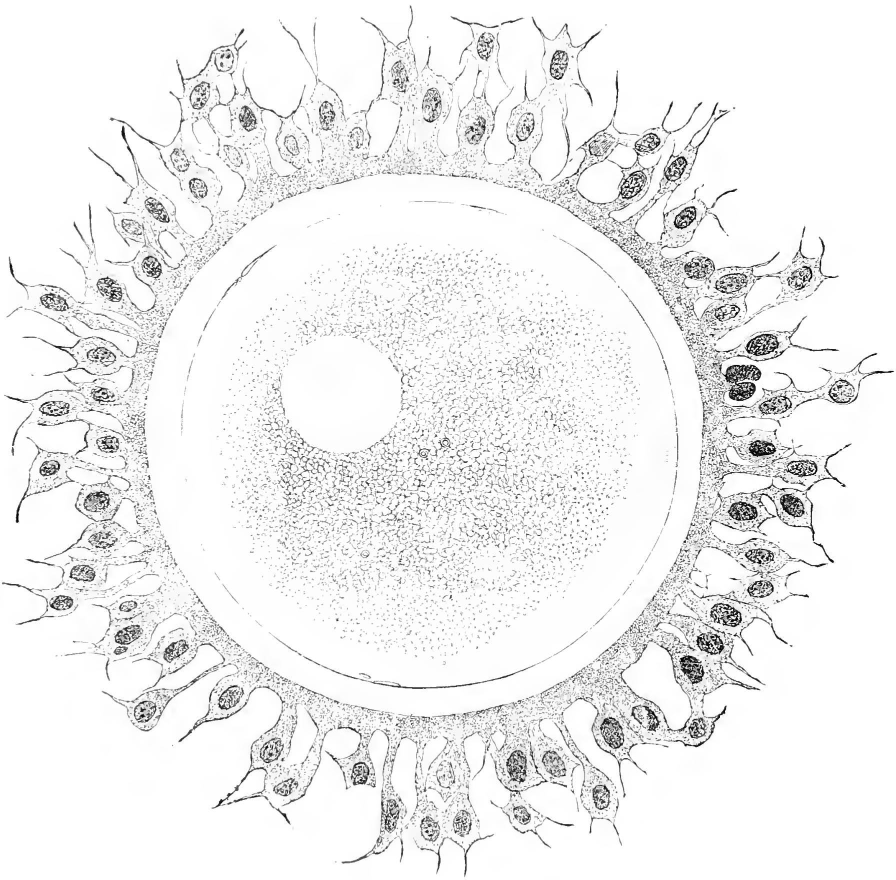


FIG. 4.—Human ovum. ×about 500. (From Waldeyer.) It shows yolk granules in the centre surrounding the nucleus (which, like other cells, contains a more deeply staining spot or nucleolus) and a clearer peripheral portion. It is enclosed by follicular epithelial cells.

all species, however, the ovum, like the spermatozoon, consists of a single cell with nucleus and external protoplasm or cytoplasm.

Both the ovum and the spermatozoon, prior to uniting together in the act of fertilisation, undergo a process of maturation. This

takes place (or at any rate begins) in the reproductive organ or gonad (ovary or testis according to the sex of the parent) and consists essentially in the reduction of the nuclear material to one-half of what it was in the unripe ovum or spermatozoon.

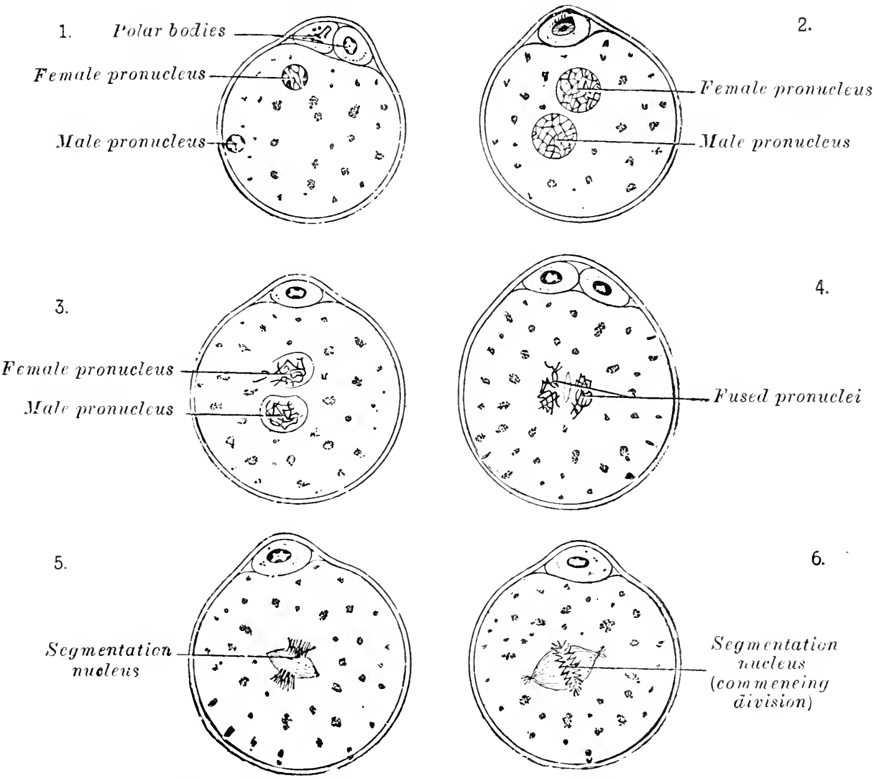


FIG. 5.—Fertilisation of the ovum of the mouse. The male pronucleus represents the head of the spermatozoon, and the female pronucleus is the nucleus of the ovum after the polar bodies (see p. 37) have been given off. (After Sobotta.) (From *Gray's Anatomy*.)

The process, which is described in some detail in a later chapter, may be regarded as an act of preparation for fertilisation when the two gametes come together and their respective nuclei also fuse, the nuclear material being thereby restored to what it was originally in the unripe gamete.

There is evidence that in some animals at least the ova and spermatozoa have a definite attraction for one another (Dakin

and Fordham). This phenomenon, which must facilitate fertilisation, is called *Chemotaxis*.

At the beginning of the act of fertilisation the head of the spermatozoon comes in contact with the ovum and then passes inward through the wall of the ovum, so that the latter at first contains two nuclei, its own and the head of the spermatozoon. Eventually the nuclei come together and fuse, as already stated, and the tail of the spermatozoon, which consists of cytoplasm, breaks up and becomes absorbed in the cytoplasm of the ovum. The oosperm or zygote formed in this way is the starting-point of a long series of cell divisions which culminate in the formation of a new completely formed individual resembling the parent individuals from which the ovum and spermatozoon were derived.

Artificial Fertilisation.—Loeb and others have shown that with the sea-urchin and many species of animals the fertilising action of the spermatozoon can be imitated by physico-chemical methods and artificial fertilisation of the ovum may take place, new individuals being produced in this way without the intervention of a spermatozoon. Thus Loeb found that by adding a little of a fatty acid to the sea-water which contained the sea-urchin eggs and then transferring the eggs to another sample of sea-water to which sodium chloride had been added, it is possible to cause the eggs to undergo segmentation or cell division, resulting in the development of new individuals. A number of other methods which are equally effective have been devised, and upon these theories have been based as to the nature of the reacting substances which are carried into the ovum by the sperm in normal fertilisation. There are many animals, however, in which the ovum alone is capable normally of initiating its own development. This condition, which was discovered by Bonnet in 1795 in the aphid or plant louse, is known as *Parthenogenesis*, and similarly artificial fertilisation has sometimes been called artificial parthenogenesis. Natural parthenogenesis is often a cyclical or seasonal phenomenon, as in the plant louse, with which the female reproduces without the intervention of the male throughout the summer, after which males appear and generation takes place sexually. This is one example of an "Alternation of Generations," a succession of asexual generations being followed in the autumn by a sexual one. In such forms as the jelly-fish and the polyp the alternation may be between one sexual and one asexual

generation. Again in other animals, such as the bee, partial parthenogenesis occurs, the female giving rise to two kinds of eggs, one kind developing without fertilisation and giving rise to drones or males, while the eggs of the other kind, which are fertilised by stored-up spermatozoa, develop into workers and queens, both of which are females.

Hermaphroditism.—In some animals which propagate sexually, instead of the ova and spermatozoa being produced by two sexual individuals, they are formed by the same individual, which is then said to be hermaphrodite or monœcious, the bisexual condition being described as diœcious. In certain hermaphrodite species the two sorts of sex cells are produced simultaneously by the same individuals, but in these the spermatozoa and ova are formed at different seasons, the individual animals sometimes functioning as males and sometimes as females. We shall return to this subject later in considering the phenomenon of sex determination.

With hermaphrodite animals in which the ova and spermatozoa are produced simultaneously self-fertilisation sometimes occurs, but cross-fertilisation (or the union of eggs and sperms coming from different individuals) is far commoner. Thus Morgan has shown that with the ascidian, *Cynthia partita*, although self-fertilisation occurs, the eggs are far more frequently fertilised by sperms from separate individuals. In another ascidian, *Ciona intestinalis*, self-fertilisation is only occasional. Both these animals are marine and the gametes are passed out into the sea-water. Amongst plants, as Darwin showed, very ingenious contrivances exist to ensure cross-fertilisation, and this method is the more usual in both the vegetable and the animal kingdom. Inbreeding, which implies the mating of animals which are of near kin, may be regarded as similar to self-fertilisation, except that the conjugating cells are one or more degrees distant in relationship, and it is noteworthy that under some conditions at any rate close inbreeding may result in eventual sterility. As already mentioned the deterioration resulting from close inbreeding has been held to be comparable to that taking place among some Protozoa when conjugation does not occur, and that in either case change of environment may prevent the adverse consequences of the lack of "fresh blood." This is a matter which we shall refer to again in a later chapter.

Contrivances Directed Towards Gametic Union.—The contrivances that exist to ensure the union of the gametes in fertilisation are very various. Among plants the most marvellous adaptations occur whereby pollen is transported from flower to flower, sometimes by the agency of insects, sometimes by the wind. Among the lower animals which live in water, on the other hand, the male and female gametes are brought together very much by chance, and union is only favoured by the contiguity of the parent organisms. In such animals fertilisation takes place in the water outside of the animal. Occasionally, however, as with sponges, it occurs inside the body cavity. But in the higher animals, where there is an attraction between the sexes, the fertilisation of the eggs is favoured by the male following the female and depositing its spermatozoa upon the eggs after they have been laid. In the cephalopod molluscs or cuttle-fish there is a contrivance of a special kind, for one of the arms of the male is modified and carries the spermatozoa in packets called spermatophores, and these, with the male arm, are discharged bodily into the female and the sperms are set free. With some fish and with the frog, though an actual copulation takes place, the male embracing a female, fertilisation is still external, occurring just as the eggs pass out of the female. The element of chance is reduced still further in the higher animals in which there is a definite male copulatory organ, the function of which is insertion into the body of the female, whither the spermatozoa are directly ejaculated, but as we have just seen the same purpose is attained in the cephalopod by the discharge of the modified male arm. It is noteworthy that in those animals which copulate the number of ejaculated spermatozoa far exceeds the number of ova. This is especially seen in mammals, where, as with man, 226 million sperms may be discharged to only one ovum.

Seasons of Sexual Activity.—It has been realised from the earliest times that the vast majority of animals, as well as plants, have certain recurrent seasons at which breeding takes place. These seasons very often depend upon environmental conditions, but apart from this factor, periodicity in breeding may be inherent in the organisms themselves, a fact which, as we shall see later, is clearly demonstrated in many of the higher animals. Among the Protozoa the organisms appear to pass through successive phases of vitality which are only partly dependent upon the

nature of the surroundings. Among the vast majority of organisms, however, periodicity in reproductive activity seems to relate entirely to recurrent environmental changes, such as the seasons, the phases of the moon, or the tides. That among large numbers of species spring and summer are the times for breeding is a matter of common knowledge, and it is equally well known that unusual warmth or cold may hasten or check the periodic development of the sexual instinct and the accompanying internal and external changes in the body. It is recognised also that where conditions are approximately uniform throughout the year, periodicity in the breeding habits of animals may often be obliterated. For instance, Semper states that few things impressed him more in the Philippine Islands than the absence of sexual periodicity among the molluscs, insects, and other land animals, and Westermarck has remarked on a similar fact in connection with the birds of the Galapagos Islands which are situated very near the equator, where conditions are the same throughout the year. The whale and certain other marine animals afford examples of the same principle. On the other hand, the extraordinary regularity among birds of the migratory movements, which are correlated with changes in the size of the reproductive organs and with the breeding phenomena generally, take place with a sexual rhythm which is often independent of temporary climatic conditions.

In many animals there are cyclical periods of generative activity occurring within the breeding season. Thus Fox states that the sea-urchins at Suez breed from spring until September, but that the genital products are developed in cycles corresponding to the lunar periods, the majority of individuals spawning their ova and spermatozoa into the sea about the time of the full moon. Fox remarks that the variation in the size of the gonads of the sea-urchin in relation to the moon's phases has long been common knowledge in the fish markets of the Mediterranean area where the gonads are used for food.

Another example of correlation between breeding habits and lunar periodicity is afforded by certain genera of marine polychæt worms called Palolos. Thus the Atlantic Palolo (*Eunice fucata*) and the South Pacific Palolo (*Eunice viridis*) swarm out for purposes of breeding twice a year (June and July with the first-named species, and October and November for the second),

and each time upon or near the day of the last quarter of the moon and with the first rays of the sun, and allied genera also show a regular periodicity in breeding.

Many other instances might be given of the adjustment of breeding habits to environmental conditions and the stimuli which these give to sexual activity, but we will content ourselves with one more example cited by Flattely and Walton. The "grunion" (*Leuresthenes tenuis*), a small smelt inhabiting the sandy shores of California, breeds in the spring from March to June. On moonlight nights during the big tides on the second, third, and fourth nights after full moon, very shortly after high tide, this fish "comes in with the sweep in the water, and, as the waves break, lies for a moment, squirms, and drops back into the wash of the next wave." At the wave margin the male and female burrow together and pair, the eggs being deposited below the surface at a point considerably above the limit of an average tide. Before the next big tide the eggs are washed out of the sand and hatch immediately, the larvæ escaping into the surf. Thus the procedure is so adjusted as to enable the fish to lay their eggs at the highest limit of the water line and out of reach of the succeeding tides.

The periodicity which is so constant a feature of sexual life among mammals is dealt with in a later chapter.

CHAPTER II

THE REPRODUCTIVE ORGANS IN THE HIGHER ANIMALS

THE organs of reproduction in man and other mammals occupy the floor of the pelvis which consists of the bony ring with its

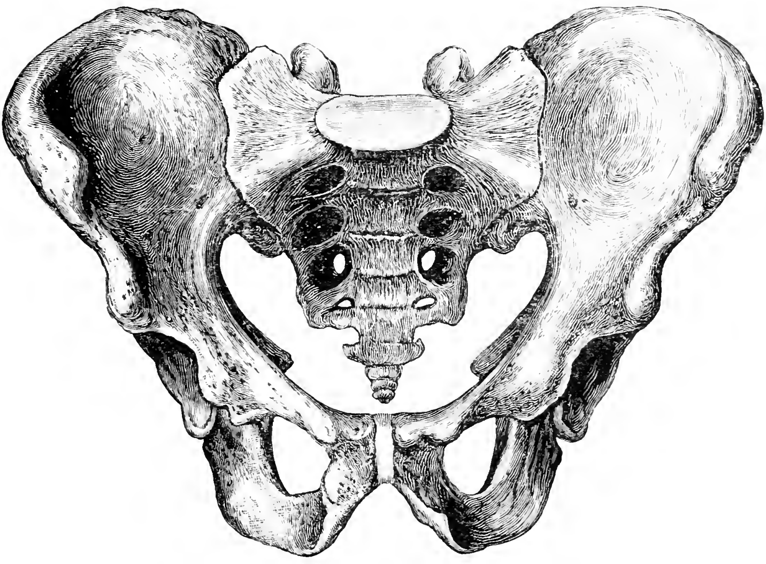


FIG. 6.—Pelvis of man; anterior aspect. (From *Gray's Anatomy*.)

contained cavity at the hind end of the body. The sacrum which is formed by the fusion of the sacral vertebræ constitutes the roof of the pelvis, and the os innominatum which consists of three bones on each side—the ilium (or hip bone), ischium. and pubis joined together—forms the floor and sides of the pelvis. On its outer surface and where the three constituent bones unite the os innominatum presents a cup-shaped cavity known as the acetabulum where the femur or thigh bone articulates with it.

Below the pelvis the os innominatum joins with its fellow on the other side at the ischio-pubic symphysis. The female pelvis differs from the male in being less massive, its bones being more delicate, its depth smaller, and its cavity shallower and wider.

The posterior part of the pelvic cavity is filled by muscle and skin, but passages are left for the openings to the exterior of the excretory and sexual organs. The anus at the end of

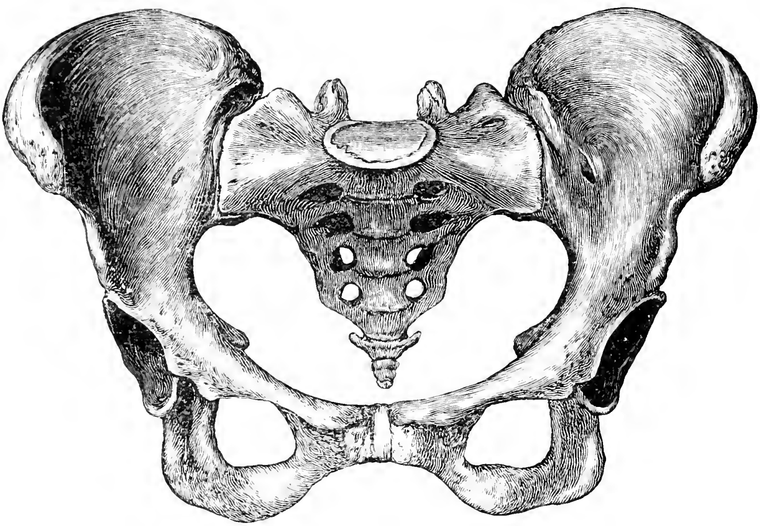


Fig. 7.—Pelvis of woman; anterior aspect. (From *Gray's Anatomy*.)

the gut opens out just below (in man in front of) the sacrum, the bladder is just above (or behind) the symphysis, and the sexual organs lie between them.

The Male Organs

The Testicle.—In man and most of the mammals the testes (or testicles) lie outside of the body cavity in a pair of pouch-like sacs which together constitute the scrotum, whither they descend in late embryonic life. The scrotum is suspended between the anus and the urogenital opening. Each sac communicates with the abdominal cavity by an inguinal canal through which pass the spermatic cord and vas deferens or seminiferous duct.

The spermatic cord contains the nerves and vessels with which the corresponding testis is supplied.

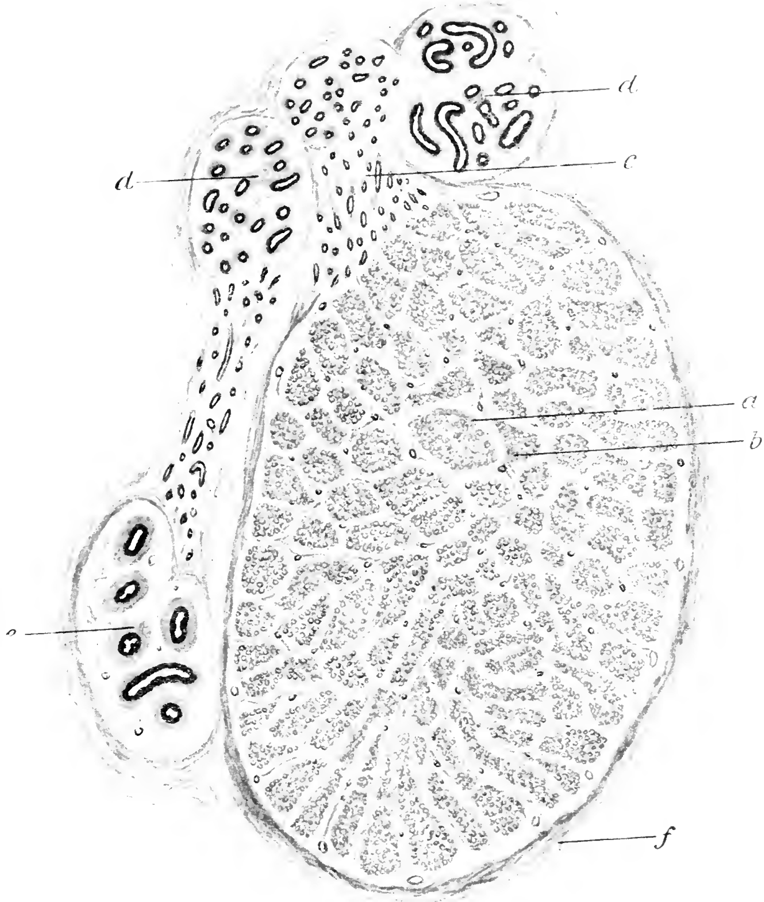


FIG. 8.—Section through testis of monkey.

a, Seminiferous tubules; *b*, interstitial tissue; *c*, mediastinum, with small tubules; *d*, vasa efferentia; *e*, vas deferens; *f*, tunica albuginea.

In the lowest group of mammals the testes remain permanently in the body cavity as they do in birds and lower vertebrates. In the Insectivora (*e.g.* the mole and the hedgehog) they descend periodically at the commencement of rut into temporary

receptacles and are afterwards withdrawn, there being no true scrotum. In some rodents (*e.g.* the hare and rabbit) the testes descend at rut into a true scrotum, and subsequently pass back

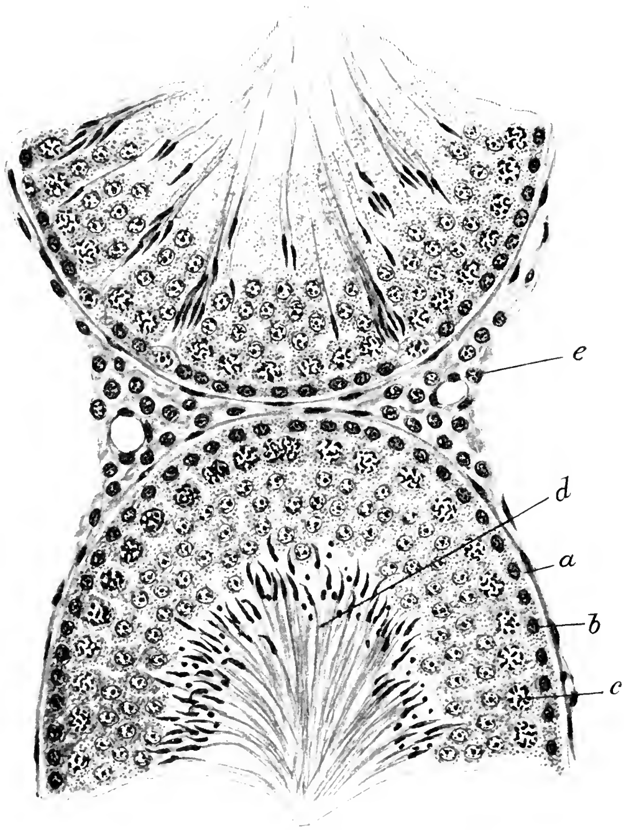


FIG. 9.—Section through portion of two seminiferous tubules in testis of rat.

a, Basement membrane; *b*, spermatogonium; *c*, spermatocyte; *d*, spermatozoa in cavity of tubule; *e*, interstitial tissue containing vessels.

through the inguinal canals. In other animals, such as the ram, there is only a slight withdrawal after rut. In man it occasionally happens that the testes retain their original position, which is approximately the same as that of the ovaries in the body cavity of the female, or more frequently they traverse only part of the

distance to the scrotum; thus the testes may reach the groin without passing through the inguinal canals, and in this position they may give rise to much discomfort or pain. The condition of retention of the testicles is known as *cryptorchism* and is usually accompanied by sterility, but in some individuals there may be a period of temporary fertility lasting for only a few years from the time of puberty and followed by permanent cessation of sperm production. This fact is of great importance to cryptorchid persons who desire to have children.

Each testis is surrounded by a serous membrane (the tunica vaginalis) and within this is a fibrous capsule (the tunica albuginea). The latter is prolonged posteriorly into the interior of the organ to form the mediastinum testis. The testicle proper, as seen in thin sections through a microscope, is composed of a large number of convoluted tubules supported by a connective tissue stroma containing blood vessels and epithelioid interstitial cells. The tubules are the essential organs which produce the spermatozoa. On the outside of each tubule is a basement membrane supporting several layers of epithelial cells (that is, of cells bounding a free surface or cavity). Inside the basement membrane certain of the epithelial cells are enlarged and form the cells of Sertoli which are supposed to have a nourishing and supporting function. Between these are the spermatogonia, which give rise by division to the spermatocytes on the inside of them. The spermatocytes divide to form the spermatids, and these become elongated out and converted into spermatozoa. (See p. 36.)

A fully developed spermatozoon is formed of an egg-shaped head, which consists almost entirely of the nucleus of the cell, a short cylindrical middle piece, and long vibratile tail. It is by the motion of the tail from side to side that the spermatozoon is propelled forward. The spermatozoa are budded off in the tubules, and thus can move freely in the fluid which is secreted by certain of the epithelial cells.

The *vasa efferentia* (or efferent ducts of the testis) are about twelve in number and open into the *epididymis*. This is a single long, convoluted tube situated at the posterior end of the testis. It is lined internally by a ciliated epithelium which is believed to exercise a slight secretory function. Its walls contain smooth muscle fibres, which contract when the contents of the epididymis

are ejaculated. The epididymis serves as the main storehouse of the spermatozoa prior to ejaculation.

The *vas deferens* is the duct which conveys the semen (or fluid containing the spermatozoa) from the epididymis to the common urogenital passage or urethra. It is lined internally by columnar epithelial cells and its wall contains smooth muscle fibres which contract in peristaltic waves when the semen is ejaculated.

The semen ejaculated through the penis, which contains the urethral channel, is the secretory product of the testes, epididymes, vesiculæ seminales, and other accessory glands. The *vesiculæ seminales* are situated at the end of the vasa deferentia, and open on each side by a common duct (formed by the union of the vas with the duct of the vesicle) into the urethra, which is the urogenital passage. Into this the bladder also opens. It was formerly supposed that the vesicles acted as seminal reservoirs, but even in such animals as the hedgehog, in which they undergo a very great development at rut, they do not contain spermatozoa. In those cases where spermatozoa have been found in the vesiculæ of human corpses, it is believed that entry took place after death, owing to the relaxation of the muscles in the walls of the ducts. It would seem probable that one of the functions of the vesiculæ is to contribute to the secretion of the medium for the transference of the spermatozoa. At the same time, it is possible that the secretion has a nutritive function for the spermatozoa, or it may exercise a stimulatory action such as has been postulated for the prostatic secretion. In the hedgehog the vesiculæ contain a large quantity of glairy, milky fluid with much crystalloid material which Hopkins has shown to consist of a peculiar kind of phospho-protein. In rodents the secretion of the vesiculæ after ejaculation coagulates and forms a plug which prevents the escape of the spermatozoa from the vagina of the female. The ferment which causes the coagulation is formed by a separate gland. The ducts of the vesiculæ unite on each side with the vasa deferentia and, as already stated, form the ejaculatory ducts which pierce the prostate gland and open into the urethra. The latter starting at the urinary bladder bends round the pelvic symphysis and is continued within the penis.

The *prostate* is a tubular gland surrounding the urethra at the base of the bladder and between that and the penis. It communicates with the floor of the urethra by numerous small

ducts. There are a number of small unstriated muscle fibres amid the glandular tissues as well as blood vessels. The secretory tubules are lined by columnar epithelium. In persons of advanced age they often contain colloid or calcareous concretions. The gland sometimes enlarges also in elderly persons and has to be removed surgically since it is apt to obstruct the flow of the

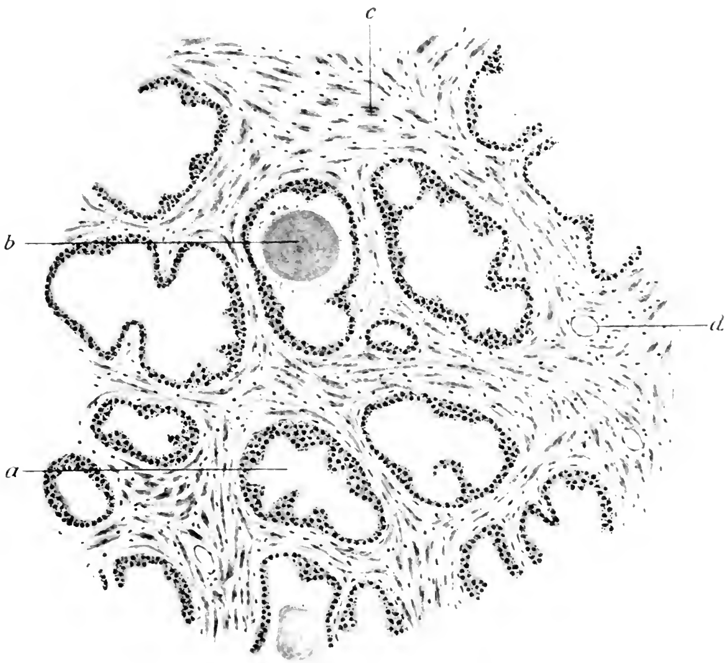


Fig. 10.—Section through prostate gland of monkey.

a, Secretory tubule lined with epithelium; *b*, tubule containing concretion in lumen; *c*, bundle of muscular fibres in connective tissue; *d*, blood vessels in stroma.

urine from the bladder, and in some cases it may give rise to abnormal or excessive sexual desire, resulting in frequent penile erections, presumably as a consequence of reflex stimulation.

The secretion of the prostate is viscid. It contains proteins and salts. Its function is not certainly known, but it is obvious that it contributes to the semen and may have some nutritive value. It is said to excite movement in the spermatozoa, for in the epididymis these cells are motionless, and, moreover, after

they have once been activated by prostatic secretion, they do not maintain life so long as when they do not come into contact with such fluid. The view that the prostatic secretion serves to cleanse the urethra of urine prior to the ejaculation of semen

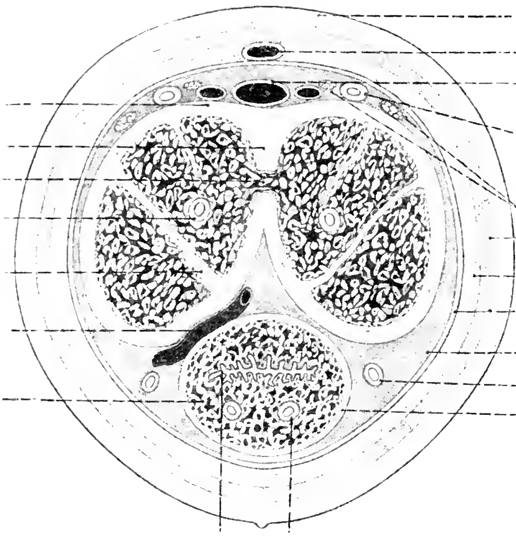


FIG. 11.—Transverse section through adult human penis. ×3. (After Eberth, from Nagel.)

A., Artery; *C.*, cutis; *Com.*, communication between the two corpora cavernosa; *Corp. Spong.*, corpus spongiosum; *F.*, fascia; *N.*, nerves; *S.*, septum; *T.A.*, tunica albuginea; *Te. Subc.*, tela subcutanea penis; *Te. Subf.*, tela subfascialis; *Tun.*, tunica penis; *Tr.*, trabeculæ of corpus cavernosum; *U.*, urethra; *V.*, veins. The tunicæ and telæ form the integument and give off the trabeculæ within.

receives support from the fact that the first fluid to escape is largely prostatic fluid and contains no spermatozoa.

Cowper's glands are a pair of small tubulo-racemose glands placed at or near the anterior end of the urethra into which they open by two ducts. They are lined internally by an epithelium which secretes a viscous fluid the significance of which is unknown. It may serve the same function as the prostatic secretion. The *glands of Littré*, which are very small, are present in the lining membrane of the urethra and contribute also to the seminal ejaculate.

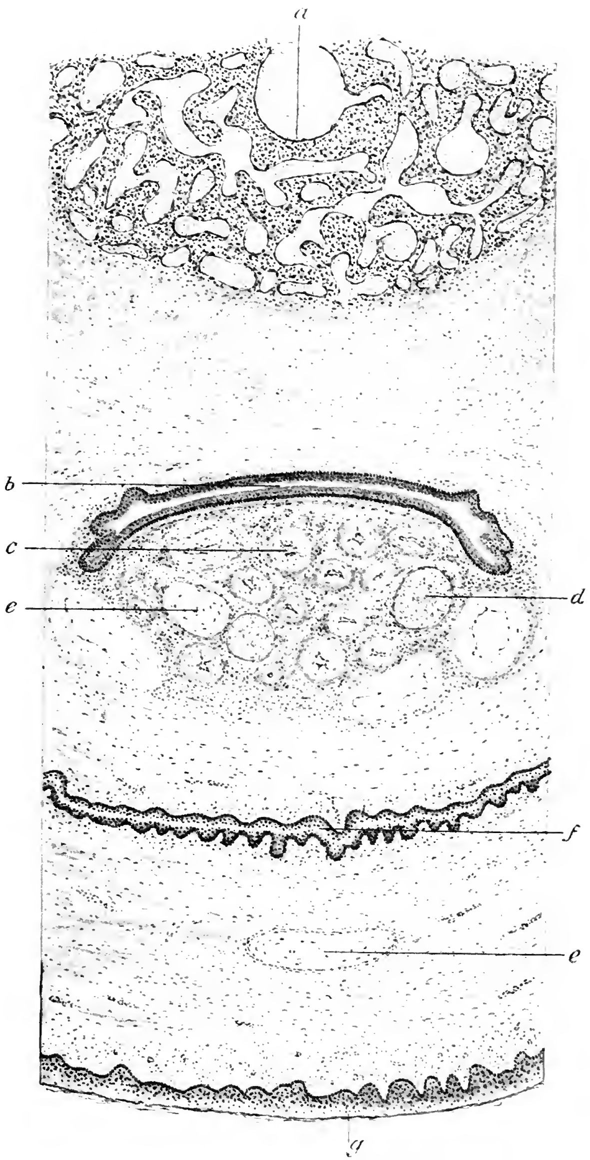


Fig. 12.—Part of transverse section through penis of monkey.
a, Erectile tissue: *b*, urethra; *c*, artery; *d*, nerve; *e*, Pacinian body (a sensory end organ); *f*, fold of epithelium: *g*, surface epithelium.

It has been suggested that the secretions of the accessory male organs may exert some beneficial influence on the female organism, and there is some evidence that they are absorbed in a quantity sufficient to produce definite effects, but whether this occurs is still doubtful.

The *penis* is the intromittent organ of copulation. In addition to conducting the urine to the exterior through the urethral channel, it serves to convey the semen (including the secretions of all the accessory glands above mentioned) into the genital passages of the female. This latter function is rendered possible by the power of erection, whereby the penis can be inserted into the vagina in the act of copulation.

The erectile tissue of the penis is mostly contained in three tracts, the two corpora cavernosa which are placed one on each side and are united in the middle line, and the corpus spongiosum which is situated internally and surrounds the urethra. The corpora cavernosa are enclosed by an integument containing fibrous and elastic connective tissue and unstriated muscle fibres, and giving off trabeculæ which divide the structures into blood sinuses or spaces. The corpus spongiosum is similar, but its fibrous framework is not so well developed. Prior to copulation the sinuses become engorged with blood, the outward flow of which is arrested by the contraction of certain muscles (the ischio-cavernosus or erector penis and the bulbo-cavernosus) at the base of the penis where they surround the bulbous enlargements of the three corpora. The glans penis at the distal end of the organ is formed by the enlargement of the corpus spongiosum.

The penis is supplied with blood by the pubic and dorsal arteries, and the veins which convey the blood away are the dorsal veins and another set communicating with the prostatic plexus.

The integument of the penis in the region of the glans becomes doubled in a loose fold. This is the prepuce or foreskin which is removed in circumcision. A number of sebaceous glands are present near the free margin of the prepuce, and these in some mammals emit an odoriferous secretion during rut. The penis is especially sensitive to external stimulation, its surface being beset with sensory end organs of various kinds, particularly in the neighbourhood of the glans.

The above description applies more particularly to the human penis, but in other mammals it has the same essential structure. In certain orders (Carnivora and Rodentia) it is provided with a cartilaginous or bony support, the os penis. Some species are provided with what are apparently sexual irritants, such as the structures which project from the penis in the rhinoceros and the tiger, and the pair of horny styles attached to that organ in the guinea-pig. In the ram and certain other Ungulata there is a peculiar filiform appendage attached to the left side of the penis which has undergone torsion, and the urethra opens to the exterior at the end of this appendage. This structure contains

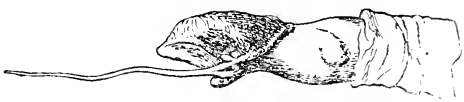


FIG. 13.—Distal end of ram's penis, as seen from the left side, showing glans and filiform appendage. The prepuce is folded back. Slightly reduced.

a pair of fibro-cartilage supporting bodies as well as erectile tissue, and its function appears to be insertion into the mouth of the uterus during copulation, since if this filiform appendage is cut off the ram is generally rendered barren.

The penis is in front of the scrotum, and behind the scrotum is the anus. The tissue between the scrotum and the anus forms the perineum, and the corresponding space in the female is similarly designated.

The Female Organs

The *ovaries* are a pair of organs lying in the cavity of the abdomen with the dorsal wall of which they are connected by the broad ligament. This stretches across the body wall in the region in question, and to it the oviducts and uterus are also attached. Each ovary, as shown in microscopic sections, is formed of stroma or ground substance of connective tissue containing blood vessels and a number of vesicles of varying sizes known as the Graafian follicles. The smallest of these—the primordial follicles—however, have no cavity, but consist of ova surrounded by a row of epithelial cells: these lie just

below the surface of the ovary. As the follicles increase in size they pass inwards to the centre of the ovary, and the epithelial cells multiply and a space is formed between those immediately surrounding the ova and the outer cells which line the wall of the follicle just inside of the connective tissue. This space becomes filled with a nutrient fluid containing proteins, etc., and called the liquor folliculi. The two parts of the follicular epithelium are, however, always connected by strands of similar

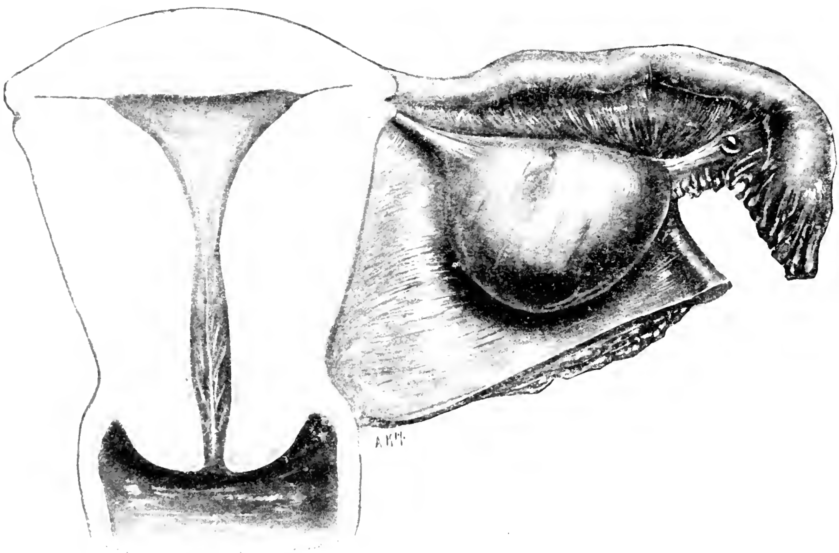


FIG. 14.—Uterus with vaginal attachment, broad ligament, Fallopian tube and ovary of the right side from a woman prior to children bearing, aged 22 (natural size). (From Bell's *Principles of Gynæcology*, Baillière, Tindall, & Cox.)

cells, so that the cells surrounding the ovum are not isolated. The innermost layer of epithelial cells has the function of transferring nutriment to the ovum. The outer wall of the follicle consists of one or more layers of connective tissue which merges in the ovarian stroma. Each follicle usually contains one ovum (rarely two or more). The largest follicles occupy a large part of a section through the ovary, and as they reach maturity come to protrude visibly from the surface. In animals which produce large litters, the ovaries may assume the appearance somewhat

of a bunch of small grapes, each grape representing a follicle. The ovaries also contain degenerate or atrophic follicles, and it is interesting to note that degeneration may set in at all stages of growth, so that atrophic follicles are of varying sizes. In such follicles the entire contents degenerate, and the cavity becomes eventually filled in by new ingrowth of connective tissue. Some of these follicles contain blood clots resulting from the rupture

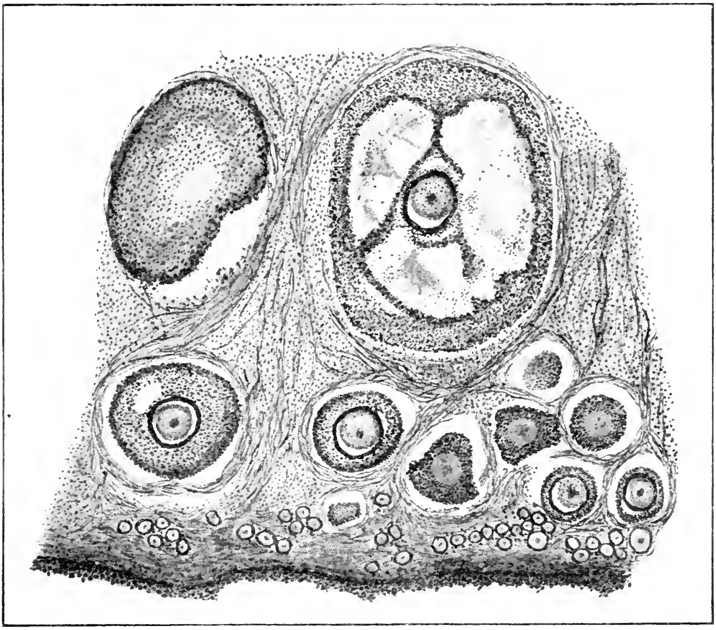


FIG. 15.—Section through ovary of rabbit, showing follicles and ova in different stages of development. (L. F. Messel.)

of the vessels in the connective tissue wall, and when this occurs (as in the rabbit) the ovum and follicular epithelium are swept to one side by the inrush of blood. The ovaries may also contain yellow pigmented bodies known as corpora lutea. The corpus luteum is formed from the ruptured follicle after the ovum has been discharged (at ovulation), the epithelial cells undergoing a great hypertrophy and becoming surrounded by a network of connective tissue which with its contained blood vessels grows inwards from the wall. Lipoid substances are subsequently

found in the enlarged epithelial cells which form the luteal cells of the yellow body. In the ovaries of many species of mammals epithelioid interstitial cells are also present in the stroma.

The *Fallopian tubes* or *oviducts*, the function of which is to convey the ova to the interior of the uterus, open internally into the body cavity close to each ovary. The discharged ova enter the fimbriæ or enlarged ends of the tubes, which are believed to expand and erect so as to receive the ova as they are released.

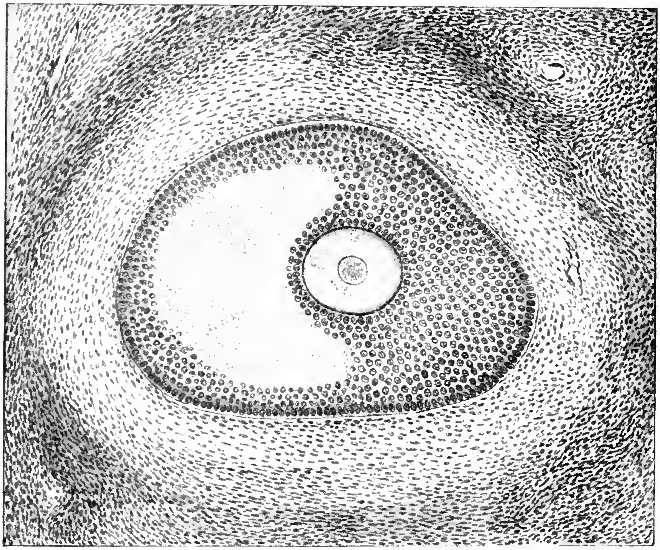


FIG. 16.—Young human Graafian follicle. The cavity contains the liquor folliculi. (From Sellheim.)

The oviducts are lined internally by a ciliated epithelium outside of which are connective tissue and unstriated muscle. Cilia are also present on the insides of the fimbriæ, their function being to direct the ova into and down the tubes which contain a certain amount of fluid secretion. In some animals (dog, ferret) the ovaries are enclosed by a membranous covering which is continuous with the tubes, an arrangement which ensures the passage of the eggs into the tubes and prevents them from becoming lost in the body cavity as occasionally happens in other species. The tubes in man are about 4 inches long.

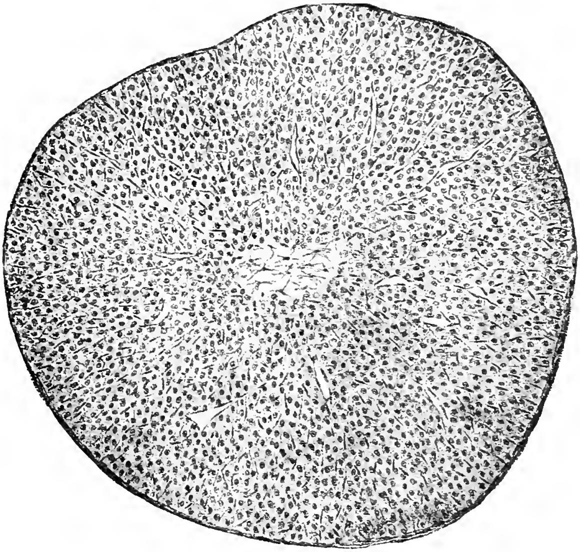


FIG. 17.—Corpus luteum of mouse fully formed. (From Sobotta.) The luteal tissue is vascularised and the central cavity filled in with connective tissue.

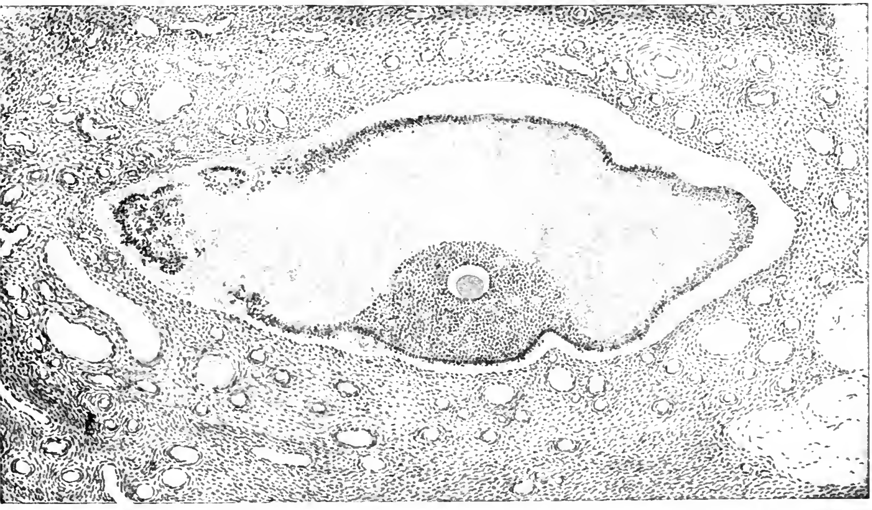


FIG. 18.—Section through follicle in early stage of degeneration. (From Sellheim.) The ovum and follicular epithelium are in process of atrophy.

The *uterus* or womb lies behind the bladder. It is the organ in which the young develop during pregnancy. In man it is a single bag, and the Fallopian tubes open into its upper corners which may be drawn out in two horns. In most of the lower mammals (mare, cow, sheep, sow, bitch, etc.) the two horns or cornua uteri are of considerable dimensions and only unite posteriorly to form the corpus uteri. In the rabbit the cornua

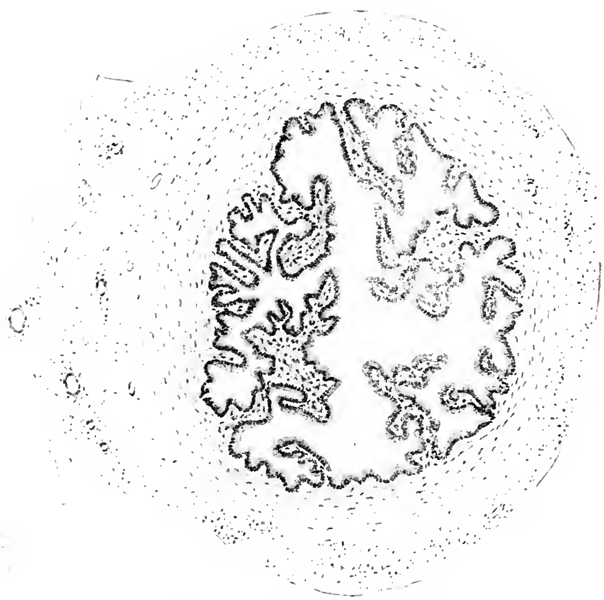


FIG. 19.—Transverse section through Fallopian tube, showing folded epithelium and muscular coat.

are separate throughout their entire length and open into the vagina through independent apertures. The virgin uterus in man is about 3 inches long. The lower (posterior) part is called the cervix. It is separated from the corpus by a constriction, the communication being called the internal os. The lower end of the cervix projects somewhat into the vagina into which it opens by the external os.

A section across the uterus (or in the lower mammals through one of its horns) shows a central cavity lined by a cubical or columnar ciliated epithelium which, together with the stroma

beneath, constitutes the mucous membrane. This contains a number of glands which open into the central lumen, and are furnished with a secretory epithelium similar to that lining the lumen. The glands are especially active during pregnancy.

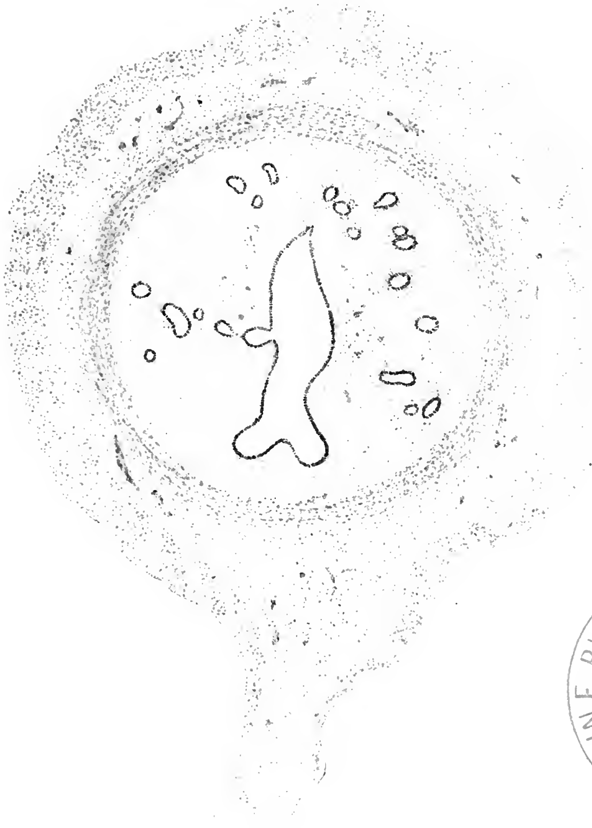


FIG. 20.—Transverse section through normal uterus of rat. (From Marshall and Jolly.)

when they secrete a nutrient fluid sometimes called "uterine milk." The stroma is a primitive connective tissue containing blood vessels. Outside of the stroma are the unstriated muscle layers (circular and longitudinal). On the outside of all is the serous or peritoneal lining.

The *vagina*, into which the penis penetrates during coitus, extends from the uterus to the exterior opening. Its walls contain longitudinal and circular muscle fibres, and internally

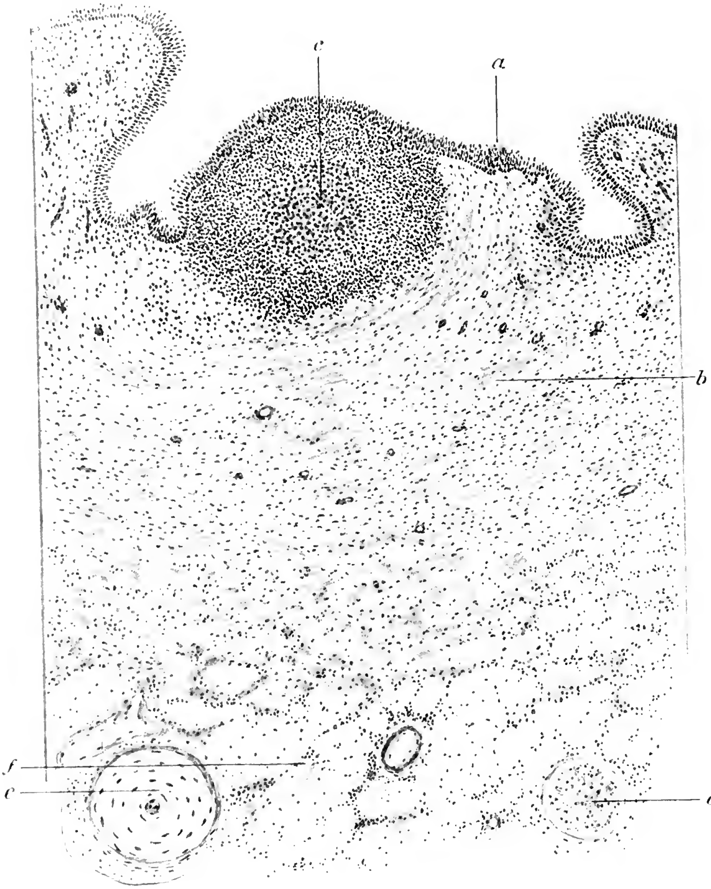


FIG. 21. Section through wall of vagina (upper part) of monkey.
a, Epithelium ; *b*, sub-mucous layer ; *c*, lymphatic gland ; *d*, nerve ; *e*, Pacinian body (a sensory end organ) ; *f*, fat cells.

it is lined by a stratified scaly epithelium, often containing a cornified layer. It opens to the exterior between the nymphæ, which are the lips closing the aperture, and lie inside the larger lips or labia.

The female sex organs, which are visible from the exterior, are known collectively as the vulva, and both the labia and nymphæ are included under this term. The labia on the outside are covered with hair. On separating the internal lips or nymphæ, not only does the vaginal opening become visible, but also that of the urethra through which the urine is ejaculated. Between the two nymphæ lies the vestibule (*vestibulum vaginæ*), which encloses the orifice of the vagina and the external orifice of the urethra. On each side of the vestibule venous plexuses —the bulbi vestibuli—are situated. Near the posterior part of the vaginal aperture there are some small mucous glands, known as Bartholini's or Tiedemann's glands, which are especially active during œstrus. The vaginal opening itself in the virgin is closed in the lower half by a membrane called the hymen, which is broken at coitus. At the other or upper (anterior) end of the vulva is the clitoris, which is a solid rod-like organ corresponding to the penis of the male, but not perforated by the urethra. It is a sensitive erectile organ and covered by a prepuce or foreskin like the penis, but it is considerably smaller than that organ. From the clitoris erectile tissue extends around the vaginal opening and beneath the skin of the nymphæ. The perineum lies between the vulva and the anus in the same position as in the male.

The *pelvic symphysis* in the female may be recognised as a slight prominence at the lower end of the abdomen and above (or anterior to) the vulva. The pelvic hair covers it. There is a cushion of fat padding it, and this is known as the mons veneris.

The Mammary Glands

The mammæ are compound tubular racemose glands. They are divisible into lobes, which are in turn divisible further into smaller components or lobules. The lobules are formed of the secretory alveoli and the convoluted subdivisions of the chief ducts with which the alveoli communicate, the whole being bound together by connective tissue. The alveoli are lined by secretory cells which discharge the substances composing the milk into more or less centrally placed lumina. During secretion the

alveoli are lined with short columnar cells from which the constituents of the milk (fat, lactose, proteins, etc.) are poured out without the cells breaking down in the process. In this respect, therefore, the mammary glands resemble the salivary glands rather than the sebaceous glands, in which latter there is actual cell disintegration in the process of secretion.

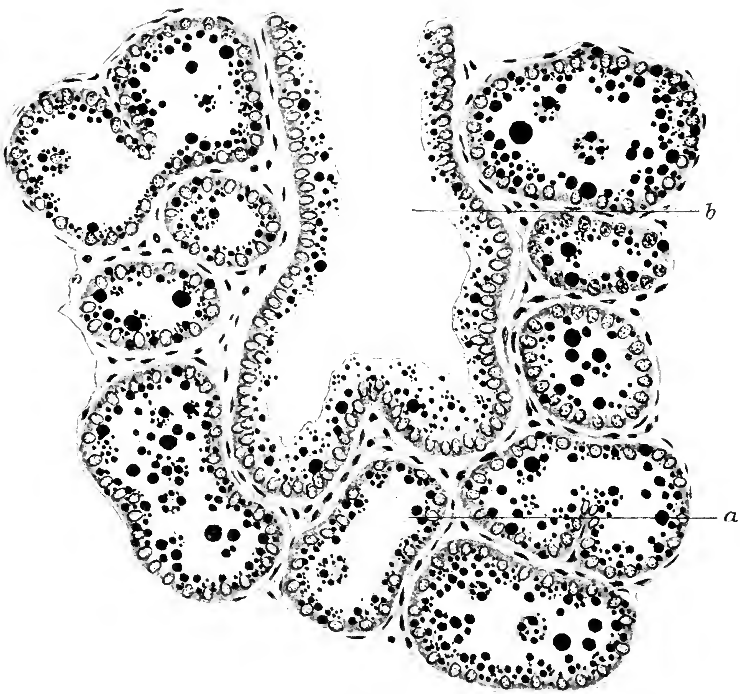


FIG. 22.—Section of mammary gland (human) during lactation (highly magnified). *a*, Alveoli ; *b*, duct.

The smaller or lobular ducts unite to form the lactiferous ducts, which are fifteen to twenty in number, and open by separate apertures on the nipple. Where the lobular and lactiferous ducts join there are dilatations which form reservoirs for the milk. In the cow there is a large milk cistern associated with each of the four teats, which in this animal, as in so many others, arise from an udder or bag containing the mammary glands. The walls of the ducts, as well as some at least of the alveoli, are

provided with unstriated muscle fibres, the contraction of which assists in the passage of the milk. The mammary glands are well supplied with blood vessels and lymphatics.

The nipples are formed of areolar tissue with unstriated muscle fibres. In the cow and many other animals the muscles are especially developed at the end of the nipple, where they form a sphincter which, when contracted, " holds up " the milk. The nipples also contain blood vessels which render them erectile. On the surface are sensitive papillæ. Around each nipple in man there is a small area of pink or pigmented skin containing minute glandular organs.

The purpose of the nipples is to facilitate the young in drawing off the milk. This is done by sucking, the nipple being enclosed by the lips of the young while the tongue of the latter is decreased in size in front and increased behind. The composition of the milk is such that it is a complete and perfect food for the young during the early stages of life outside of the mother's body.

The Maturation of the Germ Cells

It may be convenient here to refer briefly to the maturation processes which are essentially similar in both spermatogenesis and oogenesis. In each case they result in the reduction of the nuclear material or chromatin to one-half the normal amount characteristic of the body cells of the species in question. The chromatin is continued in certain filaments termed chromosomes, and is so called because it undergoes a more intense reaction under the influence of dyes of various kinds when these are applied to it. The number of chromosomes is usually constant for the cells of any particular plant or animal, though it may vary in the two sexes, the cells of one sex containing one more chromosome than those of the other sex (or the chromosomes in the two sexes may be equal in number, but certain of them different in kind). Thus in man there are said to be forty-eight chromosomes in all the body cells (or, according to Painter, forty-seven in the male and forty-eight in the female), excepting in the mature germ cells (ova and spermatozoa), and in the last stage leading up to these, where there are twenty-four. (According to Painter, however,

whereas all the ova and one-half of the spermatozoa contain twenty-four chromosomes, the other half of the spermatozoa—those which on conjugating with the ova are supposed to give rise to males—contain twenty-three chromosomes).[1]

The changes which occur in spermatogenesis may be summarised as follows: (1) A sperm mother cell or primary spermatocyte

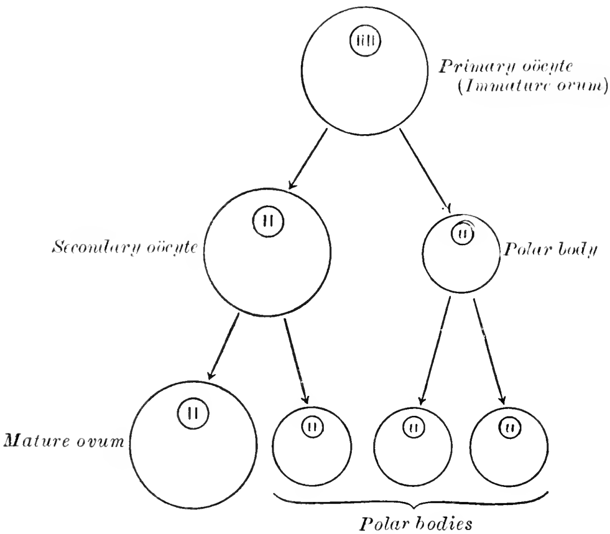


FIG. 23.—Diagram illustrating the reduction of the chromosomes in the process of maturation of the ovum. The immature ovum has four chromosomes in the case represented, and the mature ovum two chromosomes, or half the original number. The maturation of the spermatozoon is a similar process, only all the four products of division are equal and become functional spermatozoa.

divides, in which process the chromosomes do not split, so that each product of division or secondary spermatocyte contains half the original number of chromosomes. (2) A secondary spermatocyte divides, giving rise to a spermatid, and in this process the chromosomes also divide. Subsequently, the spermatid elongates

[1] As we shall see later in discussing sex-determination, in a large number of animals the reduction process may result in two sorts of spermatozoa being produced; these after fertilisation give rise respectively to the two sexual individuals in whose body cells the chromosomes differ in number or in kind.

out, the nucleus becoming shifted to one end and forming the head of the spermatozoon, which is then set free.

The maturation of the ovum differs from the corresponding process in the spermatozoon in the unequal division of the cell. In the first division, which is the "reduction division" (the chromosomes not splitting), the first polar body is extruded. This consists of half the nuclear material of the ovum, invested by a thin layer of external protoplasm or cytoplasm. The second division results in the formation of the mature ovum and the second polar body, this consisting, like the first, almost exclusively of nuclear material. In this division, as with the second division in spermatogenesis, the chromosomes undergo the usual splitting. The maturation process is commenced when the ovum is still inside the ovarian follicle, before ovulation (or the discharge of the ovum), and is continued and completed while the ovum is in process of passing down the Fallopian tube. Sometimes the first polar body divides into two equal halves, so that there are altogether three polar bodies, all of which die and are absorbed, leaving the mature ovum, with the number of chromosomes reduced to one-half, alone remaining.

It is stated that prior to the formation of the first polar body the chromosomes of the ovum unite together in pairs, and that during this process, which is called "synapsis," there is an exchange of granules between the chromosomes. A similar process is said to occur in connection with spermatogenesis. The hereditary characteristics are believed by many to be located in these granules, so that it is a matter of chance whether a particular character remains located in a chromosome, or whether it passes into another chromosome which may be ejected. In this way an attempt has been made to explain the manner of distribution of the hereditary characters among the different members of a family.

The total number of chromosomes characteristic of the cells of a particular species is restored once more by the conjugation of the ovum with a spermatozoon This usually occurs in the Fallopian tube, the two nuclei becoming fused while the tail of the spermatozoon after entry into the egg becomes disintegrated and mingles with the latter's cytoplasm.

Coition

The processes involved in seminal ejaculation and penile erection are presided over by one or more (probably two) centres in the posterior or lumbo-sacral part of the spinal cord. The condition of tumescence is brought about by stimulation of nerve endings in the penis, of which, as we have seen, it is well provided, and afferent impulses are carried by sensory nerves from this organ to the spinal cord. The stimulation is usually augmented by impulses arising in the brain and induced by the emotions of courtship. Thus the process may be said to be partly physical and partly mental. There is no doubt that the actual friction set up between the male and female sexual organs is largely responsible for the consummation of the process, involving as it does the full functional activity of all the organs in the generative tract. Eckhard and others have shown that the efferent impulses coming from the spinal cord and producing erection, travel along branches of the first, second, and third sacral nerves which are vaso-dilator in function, and if stimulated in a dog by an electric current bring about a state of tumescence.

Seminal ejaculation is brought about by a series of muscular contractions which begin in the walls of the vasa efferentia and pass to the epididymis and thence along the vas deferens. The muscles of the vesiculæ and prostate contract at the same time, and the secretions of all the accessory glands are poured out.

Langley and Anderson have shown that the efferent nerves supplying these organs arise in the lumbar region, and that their stimulation in the cat and rabbit produces a powerful contraction of the muscles of the vas and related parts.

The purpose of penile erection is to give the organ sufficient rigidity to make it easy to insert it into the vagina of the female. The friction set up by intromission causes a reflex discharge of motor impulses in the female as well as in the male, and the uterus undergoes a series of peristaltic contractions. Thus in the rabbit Heape has described a rhythmic dipping of the os into the semen in the vagina, which is thereby sucked up into the uterus. In some animals, however, the semen passes directly into the uterus. Prior to the intromission of the penis the vagina becomes flushed and moistened by the mucus which is secreted ; at the same time the clitoris erects and the surrounding

parts become turgid. In the female the complete orgasm satisfying the desire is not generally consummated so rapidly as in the male, with whom seminal ejaculation is accomplished in a few minutes or even less. The culminating point in the female orgasm occurs slightly after that of the male, and is said to be marked by the expulsion of mucus (Kristeller's mucous strands) through the os uteri. The mucus is then partly withdrawn into the uterus along with the semen. Coition sometimes takes place without the orgasm in the female being completed or even without its occurring at all, but this is abnormal, and such coitions are apt to be sterile, probably because the orgasm may be an essential factor in bringing about ovulation (or the release of the ova).

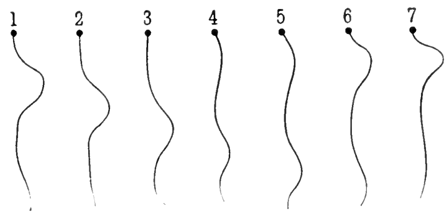


FIG. 24.—Diagram illustrating wave-like movement of swimming spermatozoon. (From Nagel.)

There is definite evidence that in some animals (rabbit, ferret, cat) ovulation is a reflex act, for it does not take place without coition. In man coition is normally performed ventrally, but it is uncertain at what stage in evolutionary history this position was first adopted.

As already mentioned the hymen of the virgin is usually broken at the first coition, before which it normally remains intact. Occasionally the hymen is of so elastic and yielding a nature that it remains unbroken at coition. Impregnation has been known to take place without actual penetration having occurred, the mobility of the spermatozoa being such as to render this possible after imperfect coition, but such cases are very unusual.

The number of human spermatozoa usually ejaculated at one time has been estimated at 226 millions, whereas in man only one ovum is usually discharged at ovulation (sometimes two, rarely three and very occasionally more). The spermatozoa make their

upward or forward progress through the uterus by the movements of their tails. Bischoff found spermatozoa at the top of the oviduct in the rabbit nine or ten hours after coition. It is in the oviduct that the ova are usually fertilised. The majority of the sperms die in the uterus, some penetrating into the glands; they become disintegrated and absorbed, or else their remains pass out again at menstruation. Whether or not the semen is absorbed in any quantity, either in the vagina or in the uterus, or in both, is a question about which there is some doubt, but it is of considerable importance in connection with contraceptive practices in coition.

CHAPTER III

THE MAMMALIAN SEXUAL CYCLE

THE season of the year when an animal of any species or variety undergoes sexual intercourse has been called by Heape the sexual season for that animal. In most or perhaps all wild mammals the male experiences such a season as well as the female, and generative activity is restricted to such times. In man and most of the domestic animals, however, the male is capable of sexual intercourse at all seasons, and spermatogenesis goes on continuously, although it is probably true that an increased activity is shown at certain seasons which may perhaps depend upon food or other environmental conditions or upon varying habits of life.

The male sexual season, when it occurs, is called the rutting season. Prior to rut the testes increase in size, and both the spermatogenetic and the interstitial tissues display activity, though the exact time relation between the changes shown by these tissues varies somewhat in different species. In those animals in which the testes are not permanently retained in the scrotum the descent takes place at the beginning of rut, and the organs are withdrawn into the abdomen when the season is over. This is the case in many rodents. In insectivores (*e.g.* the mole and the hedgehog) the testes descend periodically into temporary receptacles. In the mole it is estimated that the testes increase in size by sixty-four times, and the vesiculæ seminales, prostate, and other accessory glands likewise show an enormous growth, which is seen also in the hedgehog. The time for sexual intercourse is continuous throughout rut, there being no short periods of quiescence within the sexual season as there are in the females of many species.

In the female mammal the recurrence of the periods of sexual activity is what constitutes the œstrous cycle. The actual periods at which copulation occurs are the œstrous periods. These recur at rhythmical intervals within one sexual season,

as with the mare, cow, ewe, and sow (polyœstrous animals in Heape's terminology), or there may be only one œstrus to the sexual season, as with the bitch (monœstrous animals).

A simple œstrous cycle in such an animal as the dog has been divided into the following periods :—

Anœstrum (period of rest).

Proœstrum (period of growth, congestion, and uterine hæmorrhage).

Œstrus (period of desire).

Pregnancy *or* pseudo-pregnancy.

The complete cycle in the monœstrous dog lasts about six months, there being two sexual seasons and two " heat " or œstrous periods in one year, these occurring typically in spring and autumn.

The *anœstrum* lasts about three months, when the generative organs are in a state of quiescence. The Graafian follicles in the ovary probably undergo a slow process of growth and ripening throughout the interval, but they do not become conspicuous upon the ovarian surface until the approach of a new heat period. The uterus is relatively anæmic and the glands inactive. The mammary glands are also inactive unless lactation is in progress after a recent pregnancy.

The *proœstrum*, or period of " coming on heat," is marked by an increased activity on the part of all the generative organs. The ovarian follicles come to protrude from the surface. The uterus undergoes some amount of growth and becomes much vascularised, and the glands become active. Blood corpuscles are then extravasated within the mucous membrane and tend to congregate below the uterine epithelium. The latter ruptures in certain places, and blood is poured out into the cavity and passes down to the vagina and out to the exterior. Bleeding at the vulva may go on for a week or more. The entire proœstrum lasts for ten to fourteen days. The uterine changes involved, which usher in the period of desire or " heat " proper, have been regarded as of the nature of a preparation for the attachment of the fertilised ovum.

Œstrus is the period of desire, and coition is usually restricted to this time. Ovulation, or the discharge of the ova, takes place during this period, and the ova become mature in the way

previously described. The uterine cavity contains liquid mucus secreted by the glands, and this furnishes a medium in which the spermatozoa swim. The mucous membrane of the uterus is recuperated at those places where hæmorrhage had occurred, and external bleeding stops. The whole period lasts about a week.

Œstrus in the bitch is followed either by *pregnancy* or by *pseudo-pregnancy*. The changes which occur in pregnancy in a mammal are dealt with in the next chapter, but here it may be remarked that as far as the internal tissues are concerned there is a similarity between certain of the changes which take place under the two conditions, only those of pregnancy are more accentuated.

In both pregnancy and pseudo-pregnancy the ovarian changes are identical, at any rate in the earlier stages. At ovulation the egg along with the follicular epithelial cells immediately surrounding it and most of the liquor folliculi is discharged. The remaining epithelial cells, which constitute the majority, then undergo a rapid hypertrophy and become converted eventually into the luteal cells of the fully formed *corpus luteum*. At the same time strands of connective tissue grow inward from the wall, and these contain blood vessels. Thus the luteal cells are separated from one another by a network of connective tissue and the whole structure is richly vascularised. What remains of the central cavity of the original follicle is eventually filled in by a plug of connective tissue. The process of formation is extraordinarily rapid, only occupying a few days. The luteal cells develop to at least sixteen times the cubical content of the follicle cells, and a lipoid substance is formed within them. The corpus luteum or " yellow body " which is thus formed from the Graafian follicle after it has lost its ovum, persists throughout pregnancy or pseudo-pregnancy, but in the latter stages of the period it is in a state of regression.

After parturition the corpus luteum degenerates still further, and is eventually reduced to a mere scar.

The description as above given of the process of formation of the corpus luteum is based on that given by Sobotta for the mouse and confirmed by various investigators for many other mammals in which the phenomena are essentially similar. But the details have not been worked out in the bitch.

In both pregnancy and pseudo-pregnancy the uterus undergoes certain changes which relate chiefly to the blood vessels and glands of the mucosa. These increase in size, the whole organ assuming an appearance indicative of great activity. The secretion coming from the glands is a source of nutriment to the fœtus during pregnancy, and is similar to what in ungulates

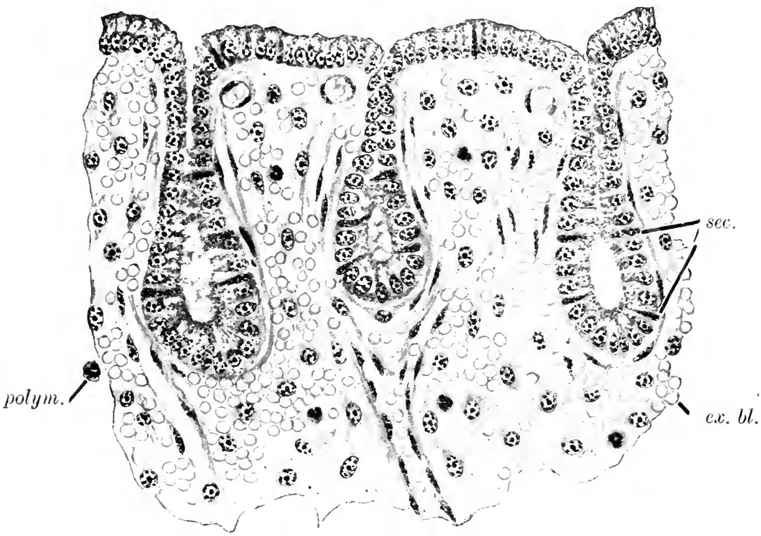


FIG. 25.—Section through procestrous uterine mucosa of dog. (From Marshall and Jolly.)
ex. bl., Extravasated blood corpuscles ; *polym.*, polymorph ; *sec.*, cells probably indicating secretory activity.

is called "uterine milk"; in pseudo-pregnancy a fluid is likewise secreted as if intended for a fœtus. The growth changes in pseudo-pregnancy are less pronounced than in true pregnancy, and are succeeded after four or five weeks by degenerative changes when the glands become shrunken, and their epithelium, from having been columnar, becomes cubical, and some of the cells are desquamated into the lumen. At the same time there is hæmorrhage from the vessels but without leading to external bleeding.

Contemporaneously with the growth of the corpus luteum and uterus, the *mammary glands* also develop during both

pregnancy and pseudo-pregnancy and active secretion generally occurs at or near the end of each of these periods, but the growth of the glands and their subsequent activity are less complete when true gestation does not take place.[1]

The gestation period in the dog is about sixty-two days, and pseudo-pregnancy may be said to last for approximately the same time or probably rather less. It does not terminate so abruptly as true pregnancy. After either period the uterus passes back to a condition of anœstrous quiescence. The occurrence of suckling which follows pregnancy favours the involution of the uterus, which in true pregnancy attains an enormous size, due largely to great muscular development. The changes which take place in pseudo-pregnancy are to be regarded, to speak teleologically, as intended to provide for fœtal nutrition and development, but do not actually serve this end owing to the ova not having been fertilised. As will be made clearer later on, both series of changes are due to a stimulus coming from the corpus luteum, which develops irrespectively of whether the eggs are fertilised or not.

Polyœstrous animals differ from monœstrous ones in having two or more short recurrent cycles within one sexual season. Thus in the sheep during "tupping time," the ewe may experience a succession of cycles, each lasting about fifteen days, until pregnancy is attained or the sexual season is over. Similarly, the mare, the cow, and the sow each experience recurrent cycles of three weeks. In all these animals the "heat" period itself is of comparatively short duration, and the actual œstrus may be reduced to a few hours as in the sheep or sometimes in the cow. The proœstrous changes are relatively slight, and bleeding from the uterine cavity is rare. Ovulation takes place during œstrus (or very shortly after, as may happen in the cow). There is no prolonged pseudo-pregnancy as in the monœstrous bitch, but the corpus luteum (which is formed as usual from the discharged follicle) proceeds with its development for from one to two weeks, and then undergoes involution, so that by the time a new period is due this structure is in an advanced state of retrogression, though still prominent on the surface of the ovary, and easily

[1] A secretion of a fluid resembling milk, but generally much thicker in the later stages, is in some animals (cow, goat) secreted during pregnancy (Hammond and Woodman, Asdell).

recognisable by its yellow colour (Corner). The uterus also undergoes changes indicative of an abbreviated pseudo-pregnancy, these consisting mainly of growth of the glands, followed by

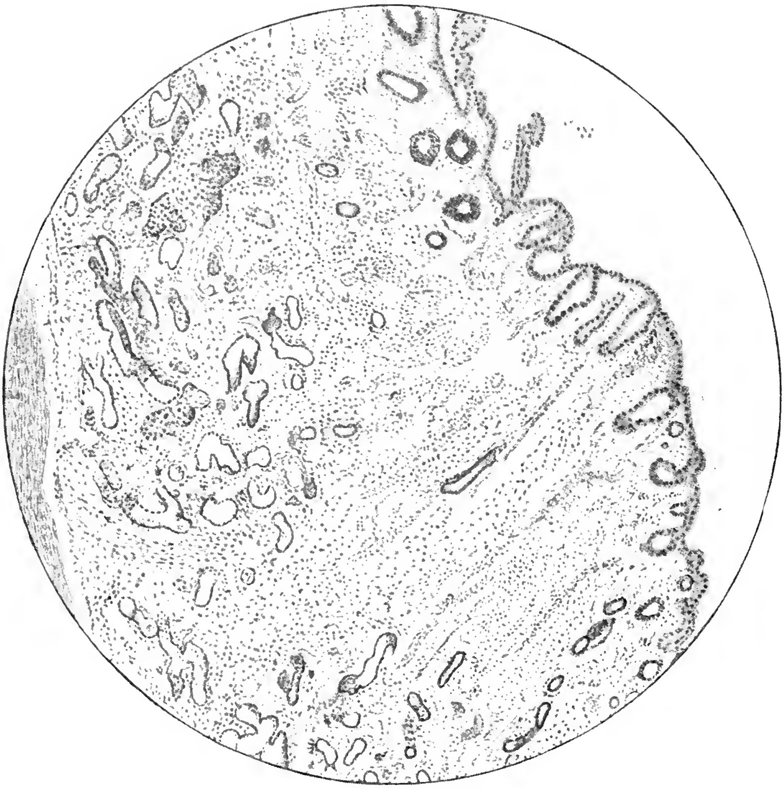


Fig. 26.—Section through uterine mucosa of dog forty-eight days after the end of proœstrum (retrogressive stage of pseudo-pregnancy). Many of the glands are degenerating; their lumina contain colloid and the remains of desquamated epithelial cells. Extravasated blood is seen in the stroma. (From Marshall and Halnan.)

regression at the approach of the next heat. Mammary changes of a similar kind have also been observed, and these, like those of the uterus, are correlated with the development and involution of the corpus luteum. In the cow bleeding, chiefly from the vagina, has been observed after œstrus, and this is believed to mark the termination of a previous shortened pseudo-pregnancy

(Hammond), as though the changes belonging to two short cycles had at this point been telescoped. The brief period of "rest" between the times of heat in polyœstrous mammals was called by Heape the "diœstrum," and the short cycle the diœstrous cycle,

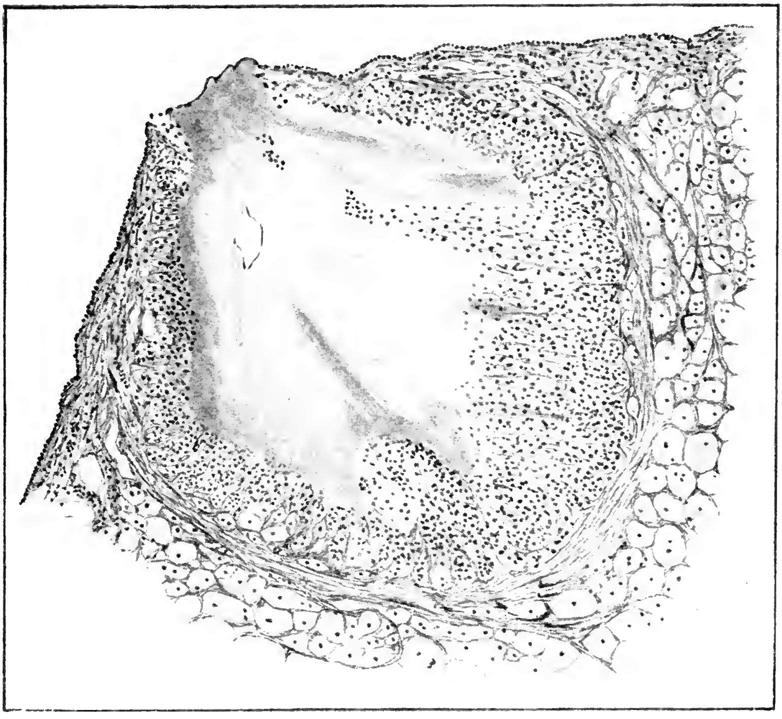


Fig. 27.—Discharged follicle of rabbit nineteen hours after coition, or about nine hours after ovulation. The epithelial cells are in process of hypertrophy and there is some ingrowth of connective tissue from the theca. The place of rupture is widely open. Hæmorrhage is slight. Outside the follicle are interstitial cells of large size. (L. F. Messel.)

but as just indicated, the changes which take place during the "diœstrum" in the ovary, the uterus, and the mammary glands seem to imply the occurrence of an abbreviated pseudo-pregnancy.

The secretion from the uterine glands at the œstrous periods facilitates the progress of the spermatozoa at this time, and it is to be noted that the contents of the cervix in cattle and horses are more liquid at œstrus than at other stages in the cycle

(Hammond). The vagina also undergoes rhythmical changes connected with those of the uterus and ovary during the œstrous cycle. These have been worked out fully by Long and Evans in the polyœstrous rat. When the uterus is distended with fluid, the mucus of the vagina is dry, but subsequently when ovulation has occurred the vaginal lumen contains a cheesy substance, the superficial epithelium and cornified layer of the wall having become completely detached. At a slightly later stage when the

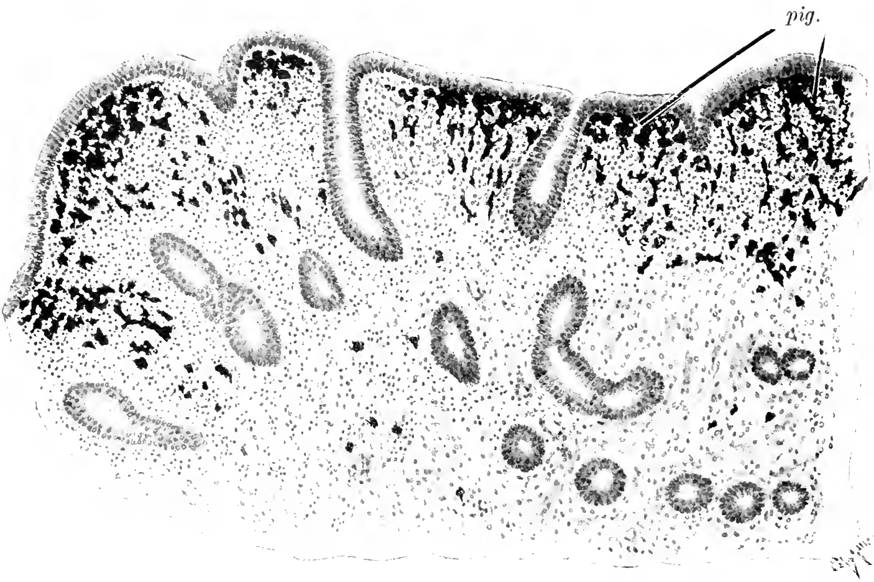


FIG. 28.—Section through portion of uterine mucosa of sheep, showing black pigment (*pig.*) formed from extravasated blood.

ovaries contain developing corpora lutea, and eggs are present in the oviduct, leucocytes are very abundant in the vagina and the surface is moist. Later on the vaginal mucosa returns to the previous condition, the epithelium being entirely re-formed.

If pregnancy takes place as a result of coition during œstrus, the corpus luteum in polyœstrous, as with monœstrous mammals, instead of degenerating after a short interval (as with the corpus luteum spurium, as it was called in the older terminology), goes on increasing in size until about the middle of the gestation period, and does not undergo regression till near the close (corpus luteum verum).

The object of the corpus luteum degenerating after a brief interval in polyœstrous animals when pregnancy has not supervened is (in teleological language) in order to admit of a fresh batch of follicles ripening, and a new heat period taking place. The purpose of the polyœstrous condition is to increase the chances of the female becoming pregnant in one sexual season, and therefore to promote the fecundity of the race. These characteristics may be supposed to have developed in evolutionary history as a result of natural selection or the survival of the fittest.

Some species of animals appear to be monœstrous in the wild state but to show varying degrees of polyœstrum under domestication. These degrees are partly racial and partly dependent upon nutrition and other environmental factors. Thus the wild sheep is said to be monœstrous, whereas the Scottish Blackface in the Highlands may have two diœstrous (or short) cycles in the absence of the male, and the same breed has five or six cycles in the Lowlands where the conditions are more favourable: various English breeds have a greater number of recurrent diœstrous cycles, the Dorset Horn sheep, owing to such an increased sexual activity, being able to have two crops of lambs in one year; while the Merinos of New South Wales experience the most extreme polyœstrum, since they are said to pass through an unbroken succession of cyclical sexual changes which, in the absence of the male, may extend throughout the year.

In addition to the domesticated animals above mentioned, the polyœstrous condition is found in a number of wild species, and appears to be especially common among rodents, but the changes which take place in the different organs have been studied chiefly in tame varieties. The guinea-pig has been shown to have a cycle of from sixteen to twenty-five days (Loeb, Stockard and Papanicolaou), the rat of four days (Long and Evans), and the mouse of three or four days (Allen). Besides the ovarian and uterine changes, Long and Evans and others, as already mentioned, have shown that there is a vaginal cycle, the cornified layer of epithelial cells being desquamated at about the time of œstrus and afterwards replaced.

Among marsupials (which constitute an order of primitive mammals with extremely short uterine pregnancy, the young being transferred at a very early stage to the marsupium or pouch),

the opossum has been shown to be polyœstrous with a short cycle of about a month (Hartman). In this animal the Graafian follicles increase to a maximum at œstrus when ovulation takes place and the corpora lutea are formed. The duration of these organs is nearly the same whether pregnancy occurs or not, and the uterine and mammary changes are indistinguishable, facts which were previously noted for the marsupial cat (Hill and O'Donoghue). Which condition obtains can only be decided by an examination of the contents of the uterus. In the marsupial, therefore, a pronounced pseudo-pregnancy associated with the development of the corpus luteum is a normal condition in the absence of true gestation. It is noteworthy that the corpora lutea degenerate completely prior to the approach of a new heat period. It has been established that the activity of the uterus and mammary glands begins some days before ovulation in the opossum in regard to both the hypertrophy and the congestion. The earlier changes are clearly comparable to the proœstrum of the higher mammals. Ovulation takes place shortly after œstrus is over, having much the same time relation as other polyœstrous animals so widely divergent as the cow and the rat. In regard to the œstrous cycle generally, it is apparent that the marsupial may be brought into line with other animals. It differs mainly in the fact that owing to the brevity of gestation (eight to thirteen days) this period is actually much shorter than—indeed, less than half of—the diœstrous cycle.

In all the animals above mentioned ovulation takes place spontaneously at or very shortly after œstrus. In the rabbit, however, ovulation only occurs after sexual intercourse (Heape). The maturation processes in the ovum also depend upon coition, and begin shortly afterwards. The actual discharge of the follicle supervenes about ten hours after coition. The maturation and ovulation processes presumably depend upon a nerve reflex set up by the female orgasm in copulation. In the absence of the buck the doe rabbit remains "on heat" for a prolonged period, and there is no "diœstrous cycle" (Hammond). Eventually, however, the enlarged follicles undergo atrophy, their cavities becoming filled or partly filled with blood which is eventually absorbed as the follicle grows smaller. The ferret resembles the rabbit in not ovulating without coition, and in

having a prolonged heat period. In the cat also ovulation does not occur spontaneously.

If a doe rabbit is allowed to copulate with a buck previously made sterile (as by cutting the vasa deferentia but without interfering with the testes) ovulation still takes places, but without pregnancy supervening. Corpora lutea, however, are formed in the ovaries, and pseudo-pregnant conditions supervene in the uterus and mammary glands, to be followed in course of time by regression and milk secretion, in the same kind of way as in the marsupial and in the bitch. Pseudo-pregnancy cannot occur normally in the rabbit owing to the fact that corpora lutea are usually only produced after a coition which results in pregnancy.

The Menstrual Cycle

The menstrual cycle in the Primates (man and monkeys) is believed to correspond to the short or "diœstrous" cycle of the polyœstrous lower mammals, but there is still some doubt as to the precise correspondence of the successive stages. It is evident that in the Primates there is no anœstrum or prolonged period of rest, but in monkeys the matter is complicated by the apparent fact that whereas these animals experience an unbroken succession of sexual cycles, each lasting about a lunar month (as in man), the periods of breeding are restricted to particular seasons (Heape).

The uterine cycle in both monkeys and man has been divided by Milnes Marshall, Heape, and others into four chief stages as follows :—

(1) The constructive stage.
(2) The destructive stage.
(3) The stage of repair.
(4) The stage of quiescence.

During the constructive stage the uterus undergoes growth, glandular development, and hyperæmia, *i.e.* increase in the blood vessels, both in size and number. The changes in a general way are described as being very similar to those which occur at the commencement of pregnancy.

At the beginning of the destructive stage the congested vessels in the uterine mucosa break down, and blood is freely

extravasated in the tissue. It subsequently forms large lacuna-like spaces in the superficial part of the tissue, and then the epithelium ruptures and bleeding takes place in the cavity. The whole, or a great part of the superficial epithelium, is removed as a result of the extensive hæmorrhage, and a varying amount of underlying stroma tissue may also be torn away, leaving the lumen of the uterus bounded by a raw edge. The discharged blood, together with degenerate epithelial and stroma cells,

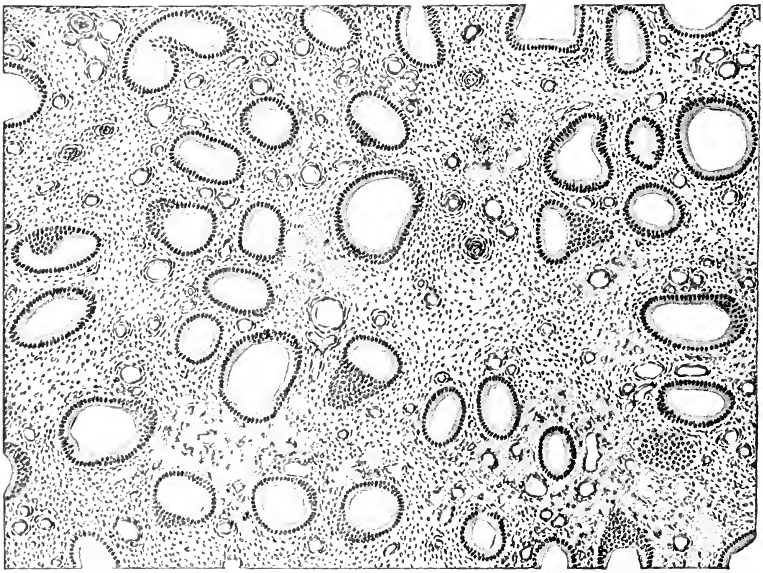


FIG. 29.—Section through mucosa of human uterus, showing pre-menstrual congestion. (From Sellheim.)

constitute the menstrual clot, and this along with a sanguine-mucous flow passes down the uterus and through the vagina to the exterior. The amount of blood lost in a woman is on an average about three ounces, and the discharge lasts from three to six days. The uterine glands are active during menstruation and contribute to the discharge. When the tissue denudation is exceptionally great the condition is known as *menorrhagia*, and when it results in a painful condition it is called *dysmenorrhœa*.

During the next period, repair sets in, the epithelium being renewed either from cells which did not suffer destruction in

the preceding period or from the cells of the glands. At this stage the blood vessels become reduced in size and number. The stage of repair is followed by a stage of apparent quiescence, but it seems probable that in many individuals the uterus commences to undergo growth changes which are continued in the succeeding constructive stage.

The constructive changes probably represent those of an

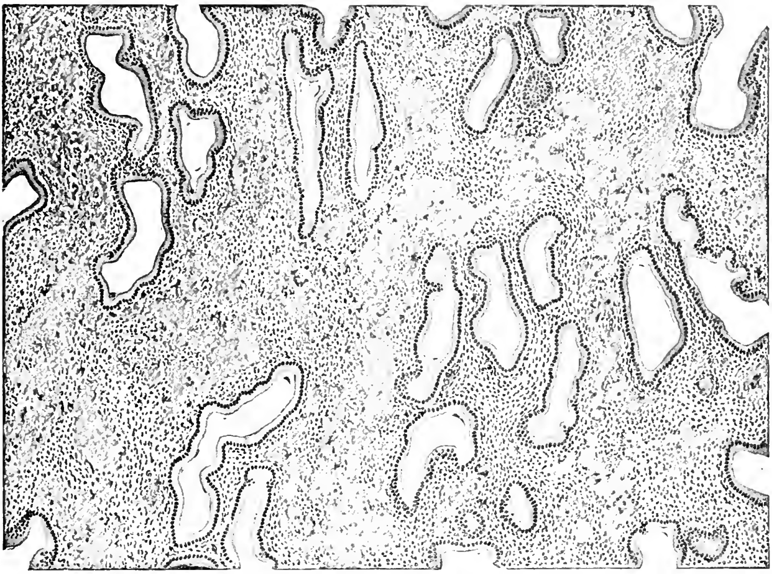


FIG. 30.—Section through mucosa of human uterus, showing extravasation of blood. (From Sellheim.)

abbreviated pseudo-pregnancy, while the destruction which follows may perhaps be the equivalent of pseudo-pregnant and proœstrous degeneration telescoped into one period. Corner has shown that in some individual monkeys in which ovulation has not occurred and there is no corpus luteum in the ovaries, the constructive processes do not take place. This is completely in accordance with what is known of the lower mammals in which pseudo-pregnant growth is invariably correlated with the presence of the corpus luteum. The monkeys, however, experience menstrual hyperæmia and destruction in spite of there having been no previous constructive changes in the uterus.

It would seem likely, therefore, that in these cases the menstrual degeneration is the equivalent of proœstrum alone, uncomplicated

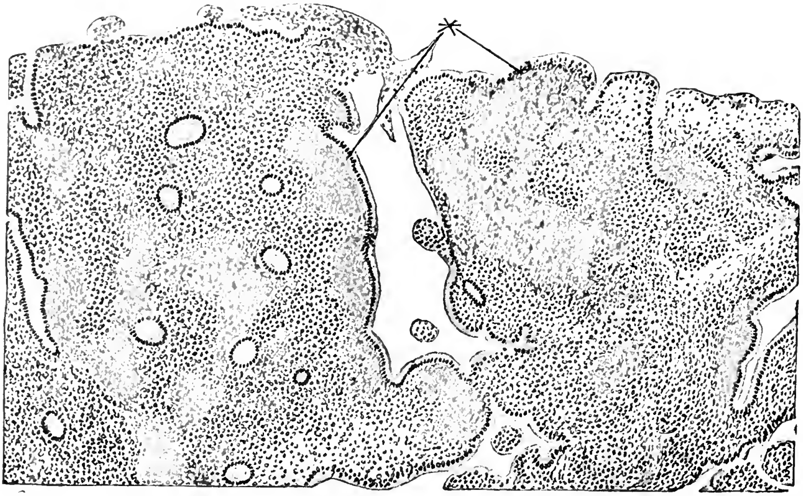


Fig. 31.—Section through mucosa of human uterus, showing sub-epithelial hæmatomata *. (From Sellheim.)

Fig. 32.—Section through mucosa of menstruating human uterus, showing bleeding into the cavity *. (From Sellheim.)

by pseudo-pregnancy. The great variation in the severity of menstruation in man may be partly accounted for in the same

way, there being some women, perhaps, who do not ovulate spontaneously and in whom consequently no corpus luteum is formed when coition does not take place and no pseudo-pregnant phenomena. It is conceivable also that with man (as is said to be the case with monkeys) there may be certain individuals who experience seasonal sterility, ovulation not occurring at all over long periods. In such women the menstrual destructive changes

FIG. 33.—Section through the human uterus during the recuperation stage. (From Sellheim.)

would naturally be less severe, since the process would represent the proœstrum alone.

The problems relating to the occurrence of œstrus and ovulation in the Primates present some difficulties. It is stated that in the macaque monkey (*Macacus rhesus*), as well as in other species, coition may take place at any time during the cycle, but the observations were necessarily made upon animals in captivity, and consequently under somewhat artificial conditions. As is well known, a similar statement is made about man. There is, however, abundant evidence that with man there are recurrent periods when sexual desire is greater than at other

times, and conversely, periods when desire is lacking. Nevertheless, there is considerable disagreement as to the stage in the cycle at which the œstrous periods occur, but there would appear good ground for stating that they are most frequent in the week after menstruation (the period being sometimes extended for a fortnight). It must be remembered that luxurious conditions favour the continuance of œstrus, and that even in some of the lower animals, when stimulated by abundant food supply (*e.g.* domesticated rabbits), coition may often occur in early pregnancy when it could serve no purpose in perpetuating the race.

In the monkey (*Macacus*) Corner has shown that ovulation takes place twelve to fourteen days before the commencement of menstruation or about ten days after its cessation (the flow lasting from four to six days). The time of ovulation may therefore correspond to a point in the cycle at or near the termination of a natural œstrus (if there ever be one), supposing œstrus to succeed the procœstrum as in the lower mammals. For man, such evidence as is available points rather in the same direction. Siegel, taking advantage of the fact that during the Great War married soldiers in Germany only had occasional leave from the army and then only for a very few days at a time, was able to obtain data as to the stage in the cycle at which women were most liable to conceive. He found that the probability of a union being fertile increased from the beginning of the menstrual discharge until six days subsequently when it reached its maximum: it remained at approximately the same height until about the thirteenth day, and then declined until the twenty-second day after the commencement of the flow; while from the twenty-second to the twenty-eighth day the unions were completely sterile. This evidence then points to the conclusion that ovulation is most frequent from the sixth to the thirteenth day (or possibly up to the tenth, since it is improbable that the discharged ova die within three or four days) after the beginning of menstruation. This time would correspond more or less to a post-menstrual œstrous period. Moreover Mall, as a result of a study of thirty-six cases of early human embryos, has come to the conclusion that fertile coition is most likely to occur between the fourth anp thirteenth day after the first appearance of the menstrual discharge.

It has been suggested that whereas monkeys apparently

menstruate periodically all the year round, they have a restricted breeding season to which ovulation is confined, and observations have been made relating to various species in the wild state and pointing to the existence of such a season. There is evidence also that for primitive man there was a restricted breeding season, as Ploss, Westermarck, and others have shown, while the variation in birth-rate in different countries, even in modern races, and the occurrence of licentious feasts and sexual orgies and ceremonies among the ancients, more particularly in the spring of the year, afford further evidence of an increased disposition to sexuality at definite recurrent intervals. The anthropological significance of these ancient feasts, which are still represented in European countries by the May Queen festivals and other similar customs, and the intimate association between them and the idea of reproduction, are fully discussed by Frazer in his book on "The Golden Bough."

Menstruation in women is accompanied by other periodic phenomena besides those directly relating to the flow. During pre-menstrual growth there may be a slight rise of temperature and a quickening in the pulse-rate as well as other manifestations of an increased metabolism. There is a swelling of the breasts, and frequently an enlargement of the thyroid, which has been known occasionally to mark the commencement of a goitre. With the actual flow these symptoms tend to subside, but they may be continued until menstruation is over. The whole period, as Head has pointed out, is one of diminution of control by the central nervous system. This is apt to result in pain which may extend to the whole body, there being a tendency to react more vividly to any excitation capable of evoking discomfort, and nervous depression is not uncommon.

Of the existence of definite metabolic changes the evidence is somewhat conflicting. Blair Bell states that there is a marked fall in the calcium content of the blood, several investigators (Schroder, Potthast, Murlin) have found a retention of nitrogen at menstruation or during the prœstrum, but the cyclical variation is not the same for all individuals.

It is a popular belief that women at the menstrual periods are liable to contaminate food in handling it for cooking, etc., owing to the emission from the skin of poisons or injurious substances which taint anything that is touched. In support of

this contention Macht and Lorbin have recently obtained evidence of the existence in the blood of a menstrual toxin which exudes in the sweat and other secretions and has a deleterious effect on living plant tissues. Thus they state that a flower held in the hand of a menstruating woman will wither more rapidly than otherwise, owing to the action of this toxic substance which is not present excepting at this stage in the cycle. The menstrual toxin is believed to affect the milk in lactating women, children sucking at such times being liable to slight digestive disturbances. A similar belief has been held about the milk of sows at the heat periods, the young pigs being said to develop diarrhœa or other alimentary troubles.

Menstruation, however, is often in abeyance during suckling (according to Fordyce, in about 60 per cent. of cases). The non-recurrence of menstruation is called *amenorrhœa.* It may be due to some pathological condition or to anæmia, arising sometimes from underfeeding. Fraenkel reported that it was common in Germany during the Great War, when it resulted from malnutrition, overwork, and general strain. A condition of amenorrhœa is said to occur normally in Lapland and Greenland during the winter, when it is clearly comparable to the anœstrum of animals.

Menstruation, as the name implies, recurs on the average in non-pregnant women every lunar month of about twenty-eight days. The cycle may, however, vary a good deal from this, and without any impairment of health ; thus it is sometimes five weeks and occasionally as short as two weeks.

Puberty and the Climacteric

The first occurrence of menstruation marks the age of puberty. This in temperate climates occurs in girls at from fourteen to fifteen, or about a year earlier than puberty in boys. In the races inhabiting warm or tropical countries, puberty is attained about two years earlier. The variation is largely racial, but partly the direct effect of environment. Luxurious living tends to hasten puberty, while inferior conditions, poor diet, and overwork may retard it.

At puberty ripe ova and spermatozoa are produced for the first time, and the gonads undergo enlargement. In correlation

with this the secondary sexual characters become accentuated; there is an acceleration of growth and an increase of strength; in the boy there is a growth of hair on the face and other parts of the body, and enlargement of the larynx and consequent deepening of the voice, processes which are not completed until about the twenty-fifth year. In the girl the pelvis widens at puberty, and the subcutaneous layer of fat which assists so largely in giving the body its graceful contour is deposited. In both sexes there are correlated psychical changes.

The menstrual cycle comes to a final end at the menopause or climacteric at an average age of forty-five, or rather earlier among the inhabitants of hot climates. Atrophic changes then take place in the ovaries, uterus, and mammary glands, and ovulation no longer occurs. Sexual desire also abates, though it may be very marked during the change, and it may persist for some time afterwards. The change lasts from three to five years, menstruation being at first irregular and then finally ceasing. The organic functions are especially irregular during the post-cessation stage. Palpitation, dyspepsia, sweating, and vaso-motor changes are common, and these are sometimes associated with hysteria, neurasthenic symptoms and mental instability. After the change is completed the metabolism settles down on a new level, and the various organs become once more adjusted so as to permit of a normal existence.

In the male there is no climacteric, sexual capacity declining gradually. It is known, however, that spermatozoa may continue to be produced in small numbers even in extreme old age, and that insemination may still be successfully performed, though the chances of a union being sterile are undoubtedly increased.

Among animals there is a period of puberty or sexual maturity just as in man, the spermatozoa and ova being ripened then for the first time. Among the domestic animals fillies will generally come "in use" when eighteen months old, cows at ten months, sheep and pigs at six, and dogs and cats at ten months, or somewhat earlier. Mice will breed at six weeks, rats at two months, and rabbits at five months. Female animals in a state of nature generally die before reaching the climacteric, but if kept in captivity or under domestication for a sufficiently long time reach a condition of permanent sterility, after which they may still retain health and a measure of vigour.

CHAPTER IV

PREGNANCY

As already mentioned, the ovum is usually fertilised in the upper or ovarian part of the Fallopian tube. The movements of the cilia lining the lumen of the tube, assisted by rhythmical contractions on the part of the muscular wall, propel the ovum along

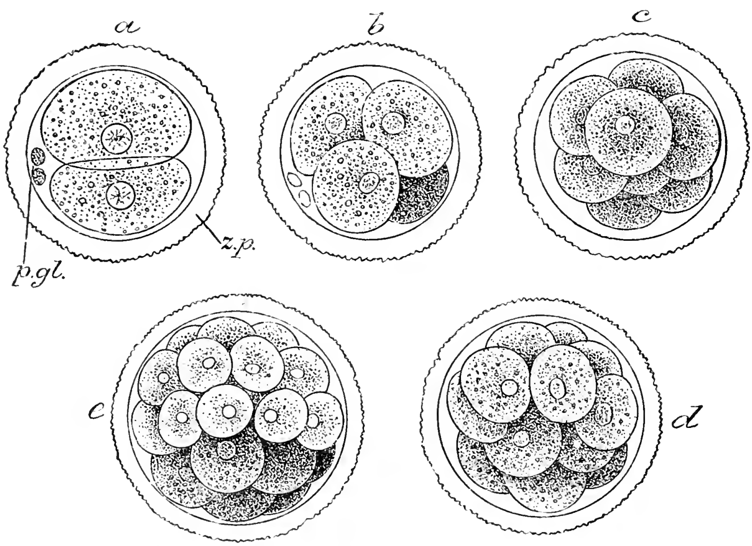


FIG. 34.—Segmentation of a mammalian ovum.

a, *b*, *c*, Earlier stages; *d*, *e*, morula stage; *p.gl.*, polar bodies; *z.p.*, zona pellucida, or outer covering of the ovum. (After Allen Thomson, from *Quain's Anatomy*.)

the tube and into the uterine cavity. The complete passage of the ovum through the tube is believed to take about seven days in man, but in the lower mammals (*e.g.* the pig), in which the question has been investigated, it almost invariably occupies four days. During its passage the ovum segments, that is to say, it divides, first into two, and then into four, eight, sixteen, and thirty-two cells, and so on until it forms a mulberry-shaped mass

of cells, known as a *morula*. By the time that the product of division has reached the uterus the morula has become converted into a hollow *blastocyst* through some of the cells in the inside of the morula becoming vacuolated, the cavities running together and then forming a space containing a fluid. Within the cavity

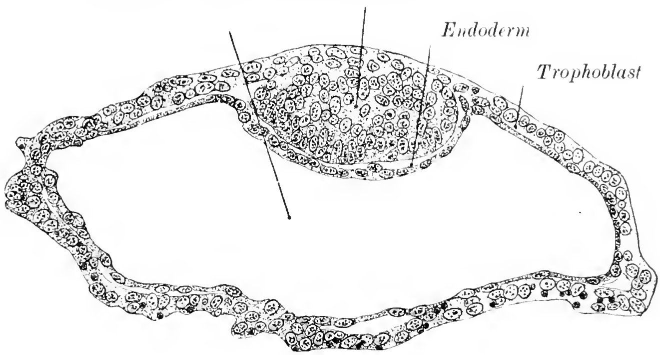


FIG. 35.—Section through blastodermic vesicle of bat. (After van Beneden, from *Gray's Anatomy*.)

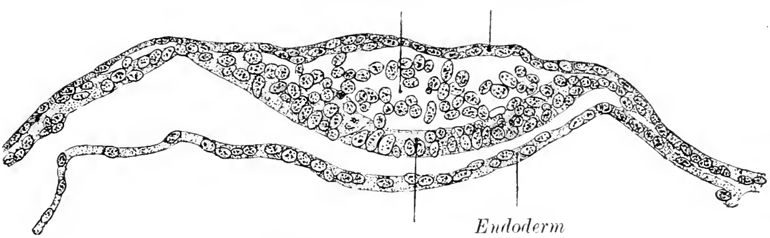


FIG. 36.—Section through embryonic disc of bat. (After van Beneden, from *Gray's Anatomy*.)

of the blastocyst a little knot of cells projects, which is called the *formative* or *inner cell mass*. This eventually gives rise to the three germinal layers of the embryo—*ectoderm*, *mesoderm*, and *endoderm*—as well as to other structures concerned in the attachment and nutrition of the embryo.

The outer layer surrounding the blastocyst takes no part in the formation of the embryo, but gives rise to a structure

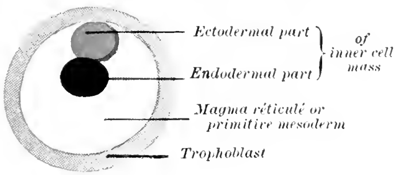
wholly concerned with the nutrition and development of the embryo. This structure is the *extra-embryonic ectoderm* or *trophoblast*; it forms the outer layer of the *chorion*, an organ of great importance, since it is by means of the chorion and the villi, which subsequently grow out from it, that the embryo is connected with the maternal placenta which is formed from the uterine mucous membrane. The trophoblast becomes differentiated into two layers, an outer one consisting of a layer of protoplasm studded with nuclei but not divided into cells—the syncytiotrophoblast (giving rise later to the syncytium), and an inner one with cell outlines—the cytotrophoblast. The mode of formation of the inner portion of the chorion is described below.

The lower or innermost layer of cells constituting the *formative cell mass* above referred to, at an early stage becomes flattened out, giving rise to the endoderm, and from the endoderm the *yolk sac* is formed as a little closed vesicle within the blastocyst. Part of its cavity (the archenteron) is eventually included in the embryo, becoming the alimentary canal. In man and the other Primates the yolk sac does not appear to exercise any function as an organ of embryonic attachment, such as it does in most mammalian orders, and notably in marsupials, in many species of which it forms the sole fœtal placental organ (or organ of fœtal nutrition).

The third germinal layer or *mesoderm* arises from the sides of the embryonic area of the blastocyst, between the embryonic ectoderm and the endoderm (see below). As it spreads out it splits into two layers with a space between them. The external layer is called the *somatopleur* and the internal layer the *splanchnopleur*. The former adheres to the inner aspect of the trophoblast, which is composed of extra-embryonic ectoderm and forms with it the *chorion* or diplotrophoblast. The splanchnopleur is applied externally to the endodermic wall of the yolk sac. The space between the two layers is the extra-embryonic cœlom, which intervenes between the chorion and the yolk sac.

In the rabbit and many other mammals the *amnion* or inner of the fœtal membranes arises by the formation of folds of extra-embryonic ectoderm together with the somatopleur in conjunction with it, the splanchnopleur taking no part in the process. The extra-embryonic cœlom is continued in the folds, each of which contains two layers. The folds grow up over the dorsal surface of the embryo and eventually meet and fuse, and when

the union is complete the outer and inner layers (each of which is composed of ectoderm and somatopleur) are separated by the cœlom. The outer layer becomes the chorion, as already described, while the inner layer is the amnion, within which is the amniotic cavity containing the embryo. In man, however,



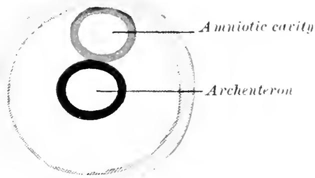


Fig. 37.—Diagram showing the first differentiation of the formative cell mass. (From *Gray's Anatomy.*)

Fig. 38.—Diagram showing the early stages in the formation of the amnion and archenteron. (From *Gray's Anatomy.*)

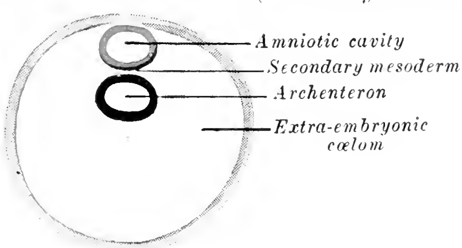


Fig. 39.—Diagram showing the commencing formation of the extra-embryonic cœlom. (From *Gray's Anatomy.*)

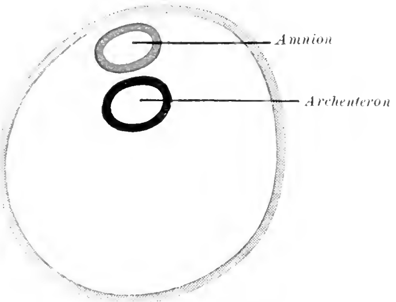
and certain other animals this cavity develops from its inception as a closed sac in the middle of the ectodermal part of the inner cell mass.

Development of the Embryo

The embryo develops from the layer of ectoderm cells lining the amniotic cavity and forming its floor and from the endoderm cells of the yolk sac lying immediately below the embryonic ectoderm. This area of cell proliferation is known as the *embryonic area.* The formation of the mesoderm has already been referred to. During the first three weeks of its existence the embryo resembles a flattened disc lying upon the yolk sac. Looked at from above, the area of proliferation appears shaded, the shading being due to the increase of cells, the three germinal layers of embryonic ectoderm, mesoderm, and endoderm being

in juxtaposition. The proliferation is greatest at one end, and extending forward from this is a band known as the *primitive streak*, running in the centre of which is the *primitive groove.* Anterior to the primitive streak there arise two folds between which is the medullary groove. The folds eventually unite, and the groove becomes converted into the *neural canal.* Above the primitive streak is the amnion, and below it is the yolk sac.

The next process that occurs is the folding off of the embryo. The cavity of the amnion becomes enlarged, and dipping down over the head, tail, and sides of the embryo, the latter is converted into a sort of tube, the inside of which is a part of the



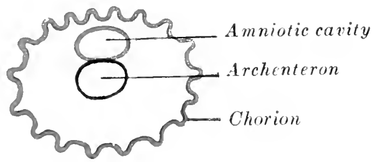
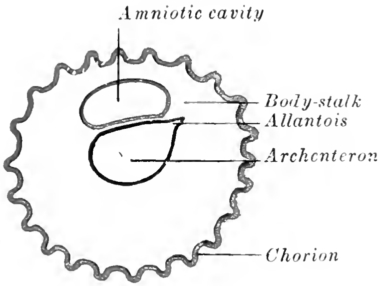


FIG. 40.—Diagram showing the extension of the mesoderm. (From *Gray's Anatomy.*)

FIG. 41.—Diagram showing a very early stage in the development of the human ovum. (From *Gray's Anatomy.*)

original yolk sac folded off from the rest of the sac. The part of the yolk sac contained within the embryo becomes the alimentary canal, as already mentioned. The part of the yolk sac outside the embryo—the *umbilical vesicle*—is connected with the alimentary canal of the embryo by the *vitelline duct.* The *allantois* grows out from the posterior part of the embryonic alimentary canal, pushing its way along the mesoderm, but in man this structure never undergoes any great development or acquires much importance; in reptiles and birds, on the other hand, the allantois extends right round the inside of the chorion and acts as a respiratory organ. The part of the allantois within the embryo eventually becomes the bladder.

With the growth of the amnion around the embryo the yolk sac and vitelline duct are brought into contact with the *body stalk* or abdominal pedicle, a portion of thickened mesoderm



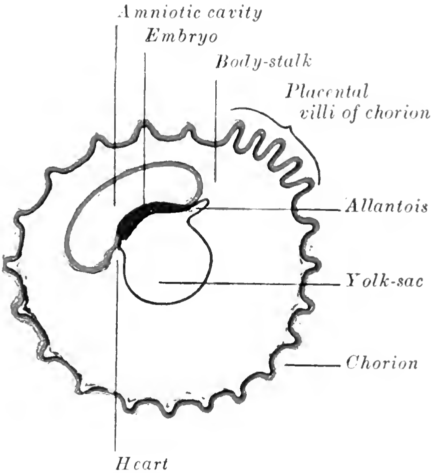
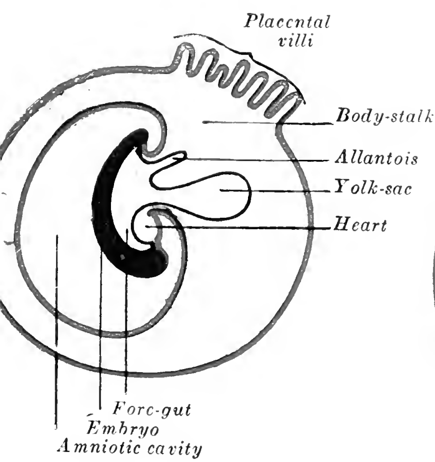


FIG. 42.—Diagram showing the early formation of the allantois. (From *Gray's Anatomy*.)

FIG. 43.—Diagram showing a later stage in the development of the allantois. (From *Gray's Anatomy*.)



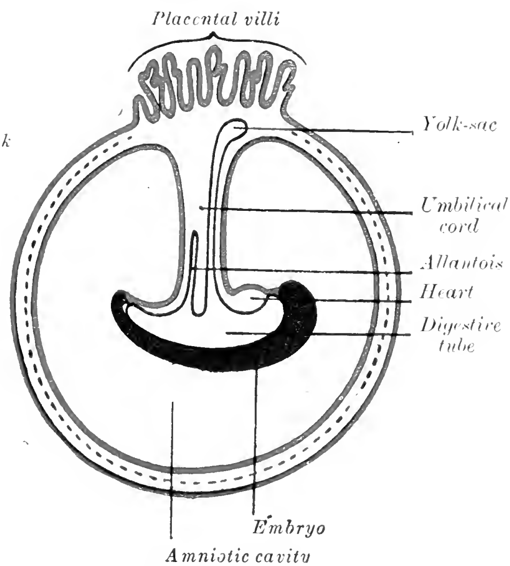


FIG. 44.—Diagram showing the expansion of the amnion. (From *Gray's Anatomy*.)

FIG. 45.—Diagram showing a later stage in the development of the umbilical cord. (From *Gray's Anatomy*.)

developed at the posterior end of the embryonic area. These structures, together with the rudimentary allantois, form the umbilical cord, and this becomes covered with embryonic ectoderm by which it is bound to the amnion. The cord constituted in this way connects the embryo with its membranes and so with the parent. It is fully developed about the sixth week of pregnancy. Owing to the growth of the hind part of the embryo beyond the original position of the cord this structure by the time of birth comes to be situated about mid-ventrally.

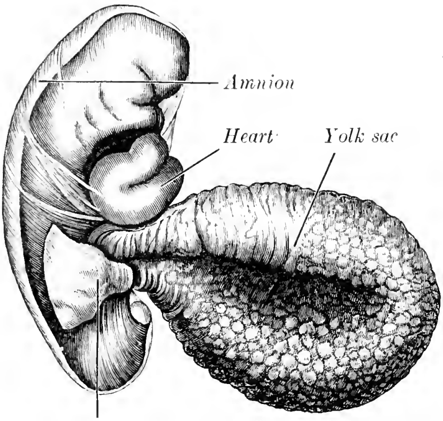


FIG. 46.—Human embryo, 2·6 mm. long.
(After His, from *Gray's Anatomy*.)

As the embryo develops, and its sides close in, some of the space between the somatopleur and the splanchnopleur becomes separated off from the rest of the space and constitutes the *cœlom* or peritoneal cavity. The further growth of the amnion results in the closing in of the space between it and the chorion. This is the condition at birth when the two membranes are still contiguous.

The growth of the amnion is accompanied by the formation of a clear fluid, the *liquor amnii*, which makes its appearance shortly after the formation of the amniotic space. By the second month of pregnancy the amniotic sac is considerably distended by the liquor. This fluid serves as a protective covering for the embryo, keeping it from the effects of jar or outside disturbance, such as injuries to the abdomen of the mother,

besides affording freedom of movement to the embryo within. The fluid is an exudation from the fœtal and maternal blood, and in the latter part of pregnancy contains urea.

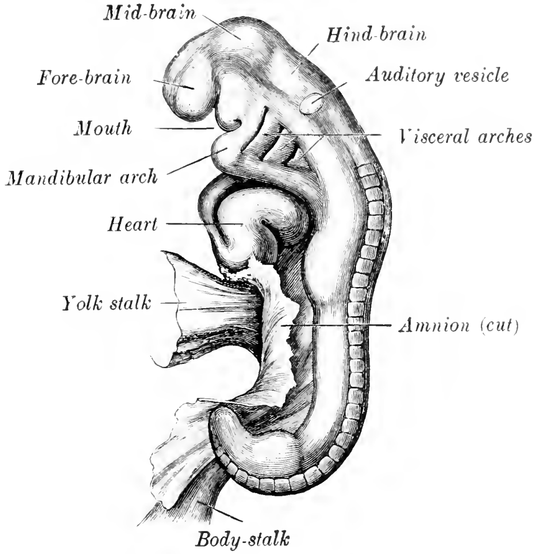


FIG. 47.—Human embryo, between eighteen and twenty-one days old. (After His, from *Gray's Anatomy.*)

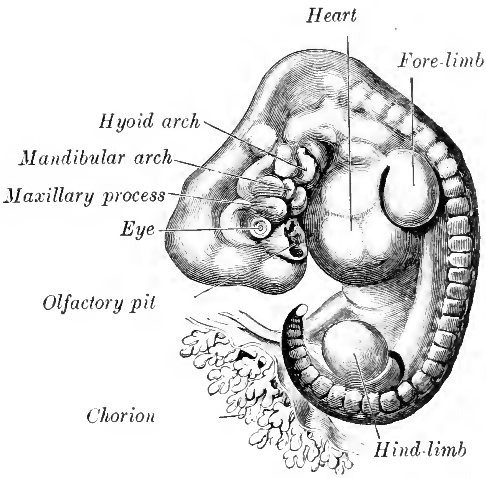


FIG. 48.—Human embryo, between twenty-seven and thirty days old. (After His, from *Gray's Anatomy.*)

The term "fœtus" is usually applied to the embryo after it has acquired something of its final shape, that is, at about the third month.

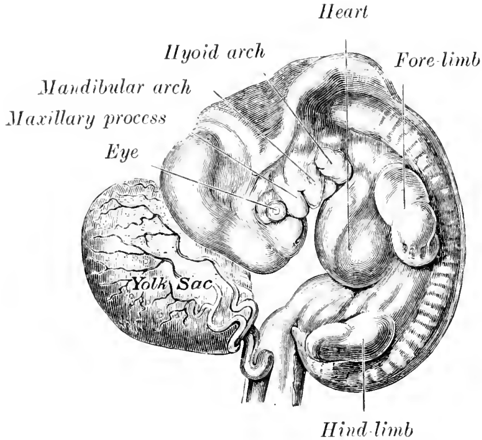


FIG. 49.—Human embryo, between thirty-one and thirty-four days old. (After His, from *Gray's Anatomy*.)

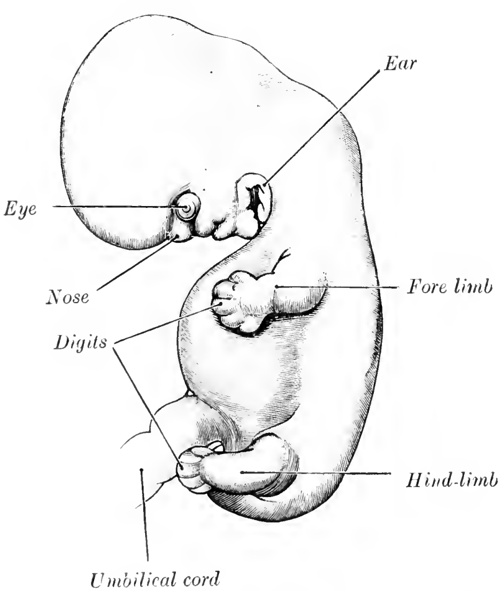


FIG. 50.—Human embryo about six weeks old. (After His, from *Gray's Anatomy*.)

The fœtus contains parts of the original three embryonic layers—ectoderm, mesoderm, and endoderm—and from each of these layers certain particular organs are produced.

The ectoderm gives rise to the epidermis and its appendages,

FIG. 51.—Human embryo, about eight and a half weeks old. (After His, from *Gray's Anatomy*.)

the epithelial structures of the sense organs, the epithelium of the nasal passages, mouth, and distal part of the urethra—the enamel of the teeth, the epithelium of the skin glands and the glands opening into the vestibule of the mouth and nasal passages, the muscle fibres of the sweat glands and those of the iris, and the whole of the nervous system.

The mesoderm gives rise to the skeletal muscles (except those just mentioned as arising from the ectoderm), the various connective tissues, the heart, the blood and lymph vessels, the

spleen and the urinary and generative organs (except the epithelium of the bladder and urethra).

The endoderm gives rise to the epithelium of the alimentary canal (except at its extreme ends) and its glandular appendages (liver, pancreas, etc.), the epithelium of the respiratory cavity, Eustachian tubes and tympanum, the epithelium of the thyroid vesicles and of the nests of the thymus, and the epithelium of the bladder and urethra (except near the external opening).

Attachment of the Embryo

In certain of the lower mammals the developing embryo remains free in the uterine cavity for a somewhat prolonged period. Thus in the cow it is still unattached on the seventeenth day of pregnancy, and its first connection with the uterine mucosa is by means of the yolk sac from which villous processes grow outwards and anchor the embryo and its membranes to the wall of the uterus. The area of attachment is also an absorbing area, nourishment being transmitted from the mother through the villi of the yolk sac. With the growth of the chorion, however, the contents of the yolk sac are gradually absorbed into the embryo, and, as we have seen, for the human embryo all that eventually remains of the yolk sac is what is represented by the alimentary canal. The attachment by the yolk sac is replaced by that through the chorion at about the fourth or fifth week in the cow, and at about the sixth or seventh week in the mare. In most marsupials (kangaroos, etc.) the yolk sac represents the sole mechanism of embryonic attachment, and after its release the young is born in an exceedingly immature condition, and forthwith transferred to the marsupium or pouch, where it is nourished through the teat.

In all the higher mammals, however (the placental mammals), the yolk sac functions for only a short time as a mechanism of attachment, and in man it probably does not function at all. We have seen that the young segmenting human ovum, even as early as the seventh day, is provided with an outer trophoblastic covering, two cell layers deep. The outer of these gives rise to the syncytium, which appears to have the power of destroying the uterine mucosa, probably by means of a ferment. By this means the segmenting ovum bores or eats its way into the

uterine mucosa where it forms an implantation cavity containing maternal blood, which escapes from the capillaries in the process of boring. The developing embryo becomes completely buried in the uterine tissue and lies bathed in maternal blood, from which it absorbs nourishment probably through the trophoblast.

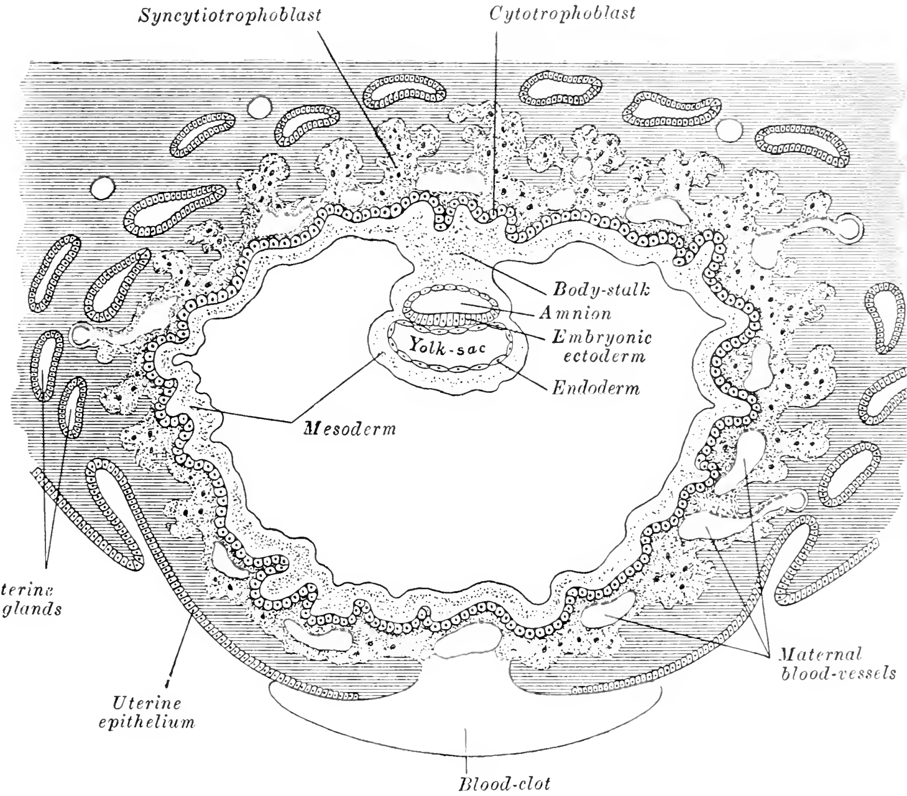


FIG. 52.—Section (semi-diagrammatic) through developing ovum embedded in the uterine decidua. (After Peters, from *Gray's Anatomy*.)

The uterine mucous membrane undergoes extensive changes as a result of pregnancy. In the immediate neighbourhood of the ovum the connective tissue cells become transformed into large oval or polygonal epithelioid cells containing large nuclei. These are called decidual cells. The process rapidly

spreads throughout the whole of the mucous membrane, and is associated with other changes in this tissue. The glands increase both in size and number and actively secrete, and the vessels become enlarged and distended with blood. The mucosa as a whole grows to four or five times its former thickness.

The part of the decidua which grows round the embedded ovum and separates it off from the uterine cavity is called the *decidua reflexa*. The closure of the decidua reflexa over the ovum is effected by a structure called the operculum deciduæ, which

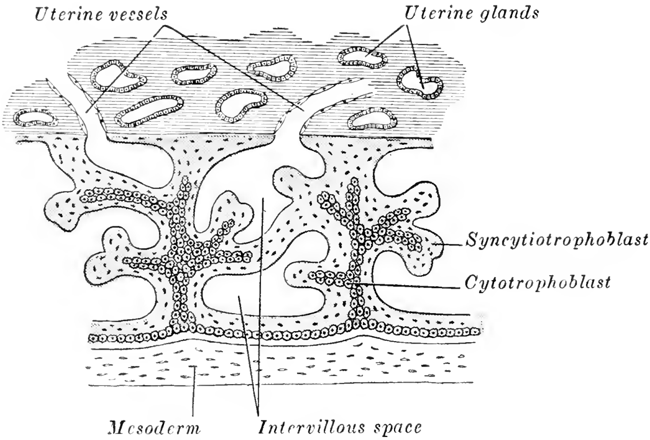


FIG. 53.—Diagram of chorionic villi into which mesoderm has not yet grown (primary villi). (After Bryce, from *Gray's Anatomy*.)

is developed from those ectoderm cells of the ovum which are last to enter the mucosa, and afterwards unites with the uterine epithelium (Teacher). The whole decidua reflexa subsequently becomes very thin and then wears away altogether, so that the outer embryonic membrane is in contact with the uterine wall. The portion of the decidua on which the ovum rests is the *decidua serotina*, and the rest is the *decidua vera*. The uterine glands, excepting for their blind ends, degenerate early in pregnancy and disappear.

The villi which grow out from the chorion project into blood sinuses in the decidua. These spaces containing maternal blood together with the decidua serotina and the outer edge of the chorion, constitute the *placenta*. This organ acts as alimentary

canal, lung, and kidney for the embryo or fœtus, but there is no actual mixing of fœtal and maternal blood, the various substances transfusing by osmosis from the blood spaces of the mother into the vessels of the chorion, the two systems of circulation being separated by only a thin cellular partition.

The blood supply to the chorion is brought by the umbilical arteries which grow out from the iliac arteries of the fœtus, and the blood is carried back from the chorion to the fœtus by the

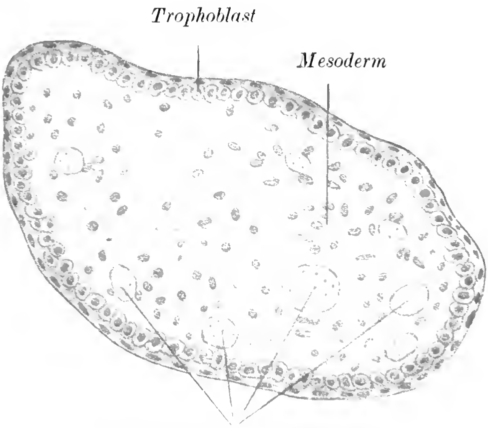


Fig. 54.—Section across a chorionic villus into which mesoderm has grown (secondary villus). (From *Gray's Anatomy*.)

umbilical vein which passes into the fœtal liver. These blood vessels develop from the mesoblastic part of the umbilical cord. It is believed that by the time the fœtal blood vessels have formed, the different cells in the body have acquired the power of selecting nutriment of the requisite kind from what is supplied by the blood. At an earlier stage, however, according to Lochhead, the trophoblast probably performs selective and metabolic functions, and so regulates the supply of nutriment in the interests of the developing embryo. Thus it has been shown that the trophoblast cells are a temporary storehouse for glycogen, fat, and hæmoglobin before these substances pass into the fœtal circulation. The avidity of these cells for special substances has been demonstrated also by *intra-vitam* staining, for pyrrhol blue, and other

dyes of a similar kind, if injected into the mother become aggregated in the trophoblast, the rest of the tissues, both of the mother and of the fœtus, being left colourless (Goldmann).

Changes in the Maternal Organism

The changes in the uterine mucosa and the formation of the placenta have been already described. In addition to these changes the uterine muscles also undergo a great development during pregnancy. The weight of the virgin uterus is only about 30 grams, while that of the uterus at the time of parturition, apart from the fœtus and fœtal membranes, is as much as 1,000 grams. Of the other characteristic changes which occur during pregnancy the development of the corpus luteum in the ovary has been already outlined. This structure develops to far greater size than the "corpus luteum spurium," though it begins to degenerate in the later stages, lipoid substances becoming deposited in great quantity in the luteal cells, but the corpus luteum does not finally disappear until after parturition. The breasts begin to swell early in pregnancy, and may even yield a few drops of milky fluid in the first months. In some animals (cow), however, there is quite a considerable amount of fluid which changes in character in the course of pregnancy, being at first thin and then thick and honey-like, subsequently becoming thinner again. The factors contributing to the mammary development and their functional correlation with the ovaries are discussed in a later chapter. The nipples increase in size and often become pigmented, and the area around them assumes slight granular elevations.

One of the earliest indications of pregnancy, apart from the cessation of menstruation, is the softening of the cervix uteri. It is not, however, until after the third month that the dimensions of the uterus have increased to such an extent that the organ rises from the pelvic cavity so as to reach the cavity of the abdomen, where it can be felt in external examination. By the end of the fifth month the uterus has extended as far as the umbilicus, and by the seventh month it has reached midway between the end of the sternum and the navel. At the end of pregnancy the uterus has reached the ribs and the pit of the stomach, the alimentary canal and other viscera being pushed

on one side in the process of enlargement. These changes sometimes produce constipation, while in the later stages of pregnancy pressure on the bladder may cause frequent micturition. The general distension often causes a cracking of the skin in the abdominal region.

Other well-known indications of pregnancy in man are the sensations of nausea sometimes followed by vomiting (the "morning sickness") which tends to occur from the second to the third or fourth month, but not afterwards, and the general circulatory disturbances which may cause hæmorrhoids and varicose veins, or induce local congestion in the face or other parts of the body. The congestion of the mucosa around the vaginal opening (Chadwick's sign) is another indication. A slight pigmentation may occur on the forehead as well as around the nipples. There is sometimes an enlargement of the thyroid gland similar to what occurs at menstruation.

The slight fluttering movements in the abdomen, commonly called the "quickening," are due to the fœtal movements being felt for the first time. They take place at about the eighteenth to twentieth week, when, owing to the increased length of the umbilical cord, the fœtus can move freely.

Duration of Pregnancy

The average duration of human pregnancy is estimated at about 270 days or ten lunar months, or rather more than nine calendar months. It is reckoned from the date of conception, or if this is not known from the cessation of the last menstruation. There is evidence that ovulation takes place most usually about the eighteenth or nineteenth day after the beginning of menstruation, so that the time for parturition may be expected, with a fair degree of accuracy on about the 288th day after the commencement of the last menstruation. It would appear, however, as already indicated, that there is a good deal of variation in the precise stage of the menstrual cycle at which fertilisation may occur. Moreover, prolonged gestation is a not very uncommon occurrence, with parturition at the 320th or even the 331st day, and twelve-month pregnancies are not unknown (Siegel). On the other hand, well-developed children may be born as early as the 240th day (Williams).

The following are the average periods of gestation among the common domestic animals :—Mare, 11 months ; cow, 9 months ; ewe, 21 to 22 weeks or about 5 months ; sow, 112 to 116 days or about 4 months ; bitch, 60 to 63 days ; cat, 56 to 63 days ; rabbit, 30 days ; guinea-pig, 62 days ; tame rat, 21 days. Prolonged gestation is not infrequent in animals as well as in man. In rodents it may be associated with the suckling of a previous litter.

CHAPTER V

PARTURITION—PUERPERIUM—LACTATION

DURING the later stages of pregnancy, and more particularly in the final week or two, the uterus shows an increasing irritability, which displays itself in more powerful contractions, giving rise to pains. With the near approach of actual labour, the fœtal membranes distended with fluid are forced into the cervix uteri, which becomes dilated, and small vessels become torn, and some blood is discharged through the genital passages. Next, the longitudinal muscles of the uterus contract and cause the external os to open. The contraction of these muscles may be said to mark the beginning of the actual labour pains and to constitute the first stage in parturition. The body of the uterus, the cervix, and the os then form a continuous passage. Typically the membranes rupture at this time, but this process may begin a little earlier or be deferred to slightly later. (Occasionally the membranes remain unruptured till after birth, the child being born inside its "caul" or "water-bag.") The amniotic fluid commences to escape, but only a portion of it. In a normal presentation the head of the fœtus comes down into the cervix and closes the external os. This marks the termination of the first stage of labour.

The uterine muscles again contract forcibly, and not merely the longitudinal muscles, but also the circular muscles as well as those of the abdominal wall and the diaphragm. These contractions expel the fœtus from the uterus to the vagina and thence to the exterior, the final propulsion being due chiefly to the contractions of the abdominal muscles. The vagina is very yielding, and the passage of the fœtus through it is facilitated further by a copious secretion of mucus. The perineum yields by stretching as the fœtal head passes out, but it is often torn considerably, and the torn edges may have to be stitched together after parturition is over. What is left of the hymen is usually

torn away, but very occasionally there is an intact hymen, even after parturition. Typically the back of the head is turned towards the pelvic symphysis. The bones of the head are somewhat compressible, and there is generally just sufficient room for it to pass through the bony pelvic ring without undue strain. Very occasionally the head is too big to traverse the passage and the child's life may have to be sacrificed to preserve that of the mother. The body of the fœtus passes out more easily, for the shoulders are more readily compressible. The umbilical cord by which the child is attached to the placenta is severed by the attendant about 1 or 2 inches from the child's navel; the child then begins to breathe and frequently emits a cry. Its body is almost completely covered by the lanugo hair, which comes away shortly after, together with a certain number of dead epidermal cells and products of secretion from the skin. The birth of the child marks the end of the second stage of labour. As soon as the child is born the remainder of the amniotic fluid escapes, and this is usually stained with blood.

The uterine contractions then cease, but are renewed after a short but somewhat variable interval. As a result of the contractions the placenta or after-birth is first separated from the interior of the uterus and then passed into the vagina, whence it is finally expelled by the action of the muscles of the abdomen. During this process, which constitutes the third stage of labour, there is some bleeding, the quantity of blood lost being, on an average, about 300 c.c., or rather less. The further contractions of the uterus gradually facilitate the closing of the torn blood vessels. The fœtal membranes are expelled with the placenta and also the remainder of the umbilical cord which is attached.

The duration of labour is about six hours longer in the case of first pregnancies than in later ones. In the former the three stages take about sixteen hours, two hours, and a quarter of an hour respectively, and in the latter eleven hours, one hour, and a quarter hour. At the commencement of labour the "pains" occur at intervals of about fifteen to thirty minutes and gradually become much more frequent so as to take place every two or three minutes. Each contraction lasts from thirty to ninety seconds, but the actual sensation of pain is considerably briefer. The force exerted at each contraction is very

great, yet it has been much exaggerated; thus Sterne in "Tristram Shandy" refers to it as equivalent to a weight of 470 lb., but modern investigations, by means of a mechanical apparatus (a dynamometer, or rubber bag fitted with a mercurial manometer), indicate that it is very much less—perhaps about 30 lb.—but show a wide variation.

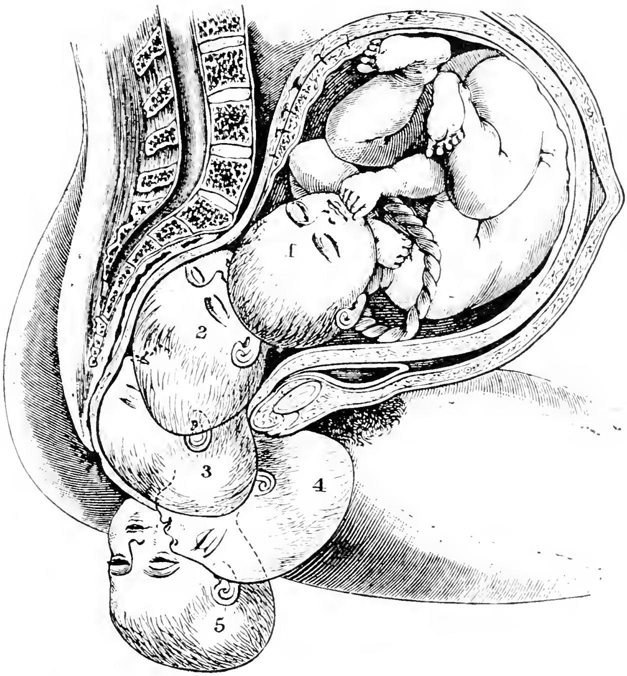


FIG. 55.—Normal birth. The figures 1 to 5 show the positions of the head during successive stages. (From Galabin's *Manual of Midwifery*, J. & A. Churchill.)

When twins are born the second child is usually expelled within half-an-hour or so after the first, but the interval may be greater.

There are other modes of presentation than the typical one described above in which the head is expelled first, and there are many variations of these modes. If the head is prevented from coming down in the normal manner, owing possibly to irregularity in the pelvis, some part of the pelvic portion of

the fœtus may appear first (breech presentation), or the fœtus may be presented crosswise. In such cases skilled assistance is necessary in order to bring about a satisfactory delivery.

The Nervous Mechanism of Parturition.—The uterus is innervated from the lumbar part of the spinal cord, the fibres coming by the second to the fifth lumbar nerves and from the hypogastric. The process of parturition depends normally on the integrity of the spinal cord which co-ordinates the various muscular movements. The uterus, however, even in the virgin, undergoes more or less rhythmical contractions, independently of its nerve connections. Thus the uterus of a bitch or other animal will do so after removal from the body, provided the organ is maintained at the normal temperature and suspended in a suitable saline fluid. Goltz showed that the bitch may give birth to pups after the complete exsection of the spinal cord in the lumbo-sacral region, the unco-ordinated contractions of the uterine muscles being sufficient to induce expulsion. An experiment by Sir James Young Simpson, the distinguished discoverer of the anæsthetic properties of chloroform, on a pregnant sow, provided a curious demonstration of incomplete parturition after the experimental destruction of the posterior part of the spinal cord. The entire litter of young pigs, excepting for the last, was expelled by uterine contraction alone, the abdominal muscles taking no part in the action owing to the absence of nervous connection. The last young one, however, remained in the vagina, owing to the abdominal muscles not acting, there being no other young ones in process of being pushed out of the uterus to propel the remaining pigling through the external opening. The various cases on record (Brachet's, Routh's, etc.) in which conception took place in women suffering from paraplegia (spinal paralysis) and was followed in due course by parturition illustrate further the possibility of the process occurring in the absence of co-ordination by the central nervous system. Under such a condition parturition is attended with difficulty and yet may be successfully accomplished.

The Cause of Parturition

As regards the immediate cause of parturition, various theories have been put forward in past times, but none of them have

ever been regarded as complete or satisfactory. As to why the uterus, after having borne its burden so tolerantly and for so long, should suddenly be thrown into violent contraction, has remained a mystery, at any rate until quite recently, but, as we shall see later, there is now evidence that the cause is to be sought for in the rhythm of the endocrine activities of the ovary. It has been known that even the virgin uterus undergoes faint contractions at more or less regular intervals, and that these may increase in force at the periods of menstruation, when the ovaries are more active. Moreover, recent investigation has shown that the ovarian influence upon the uterus is inhibited during pregnancy when the corpus luteum is a dominating factor, but that as this structure declines the uterine contractions gain in force, the expulsion of the fœtus being the culminating effect. It would appear probable that the ovary does not act directly upon the uterus but rather through the intermediation of the pituitary gland. This is a matter to which we shall return in the next chapter when considering the ovary as an organ of internal secretion.

The Puerperium

The puerperium or " lying-in " period usually lasts from about ten days to three or four weeks. It is the time when the lacerated uterine mucosa becomes healed, and the whole uterus undergoes rapid involution, but it never regresses to the size of the virgin uterus. It is important that the lying-in period should not be imprudently shortened, as, apart from the danger of " prolapsus uteri," which may occur as a result of undue exertion after delivery, the whole body is in need of rest and recuperation. It is to be noted, however, that among labouring women and others who are exceptionally healthy and strong, the lying-in period may be considerably shortened, whilst among uncivilised races there is often hardly any puerperium at all. Still more so is this true of the lower mammals.

There is generally a slight rise of temperature on the third day after labour, but this is merely indicative of some metabolic disturbance of a febrile nature on the part of the mother, and should very soon subside. If, however, owing to want of proper cleanliness the bleeding uterine mucosa becomes infected,

septicæmia or puerperal fever may result. This condition is, of course, abnormal and may be dangerous, requiring immediate medical treatment.

The normal discharge of blood and mucus from the interior of the uterus lasts for about two weeks after parturition. It is called the *lochia* and varies considerably in amount in different individuals, any quantity between ten and fifty ounces being normal. For the first few days after parturition the lochia consists largely of blood, but it gradually becomes paler, and later is composed almost entirely of mucus with which secretions from the cervix and vagina mix. The occurrence of a persistent discharge consisting largely of white corpuscles is abnormal but not very uncommon. It indicates a local lesion which has become infected.

The involution of the uterus occurs rapidly in the first few days after delivery, and then becomes more gradual, being completed after from five to eight weeks. Thus the freshly delivered uterus weighs about 1,000 grams or 2 lb. (as compared with 30 grams for the virgin uterus), but a week after parturition the organ weighs 500 grams, and at the end of the puerperium as little as 60 grams or 2 oz. By the tenth day after parturition the uterus becomes once more confined to the pelvis and cannot be felt above the symphysis. The process of involution relates chiefly to the muscle walls, the size of the cells being diminished, while the vessels become more compressed.

Lactation

The structure of the mammary glands has been described in a previous chapter. These glands, prior to conception, consist of a few ducts in the immediate neighbourhood of the two bilaterally situated nipples. In the human female it is not until the beginning of pregnancy that they undergo any true growth, such apparent hypertrophy as they appear to show at the menstrual periods being confined mainly or entirely to an augmented vascularisation and a slight increase in the number of the ducts. After conception a rapid hypertrophy sets in, the actual gland cells undergoing division and multiplication, and new secretory alveoli are formed, while the nipples also develop more fully. New alveoli are formed from those already in

existence as well as a large number of new ducts. After the second month the breasts are said to offer a nodular sensation on palpation, this being due to the growth of the mammary alveoli. The nipples also enlarge and become more erectile and are often pigmented, while the tissue surrounding the nipples becomes broader and likewise pigmented. The hypertrophy of the sebaceous glands in the immediate vicinity results in the formation of the so-called glands of Montgomery, which appear as small rounded elevations. A slight amount of milky fluid may occasionally be secreted even in the earlier months of pregnancy, but true milk is not produced until after parturition (see above, p. 74). On the first two or three days after parturition the fluid is thick and of a yellow colour. It is said to have a purging effect on the infant, who consequently loses weight, to be made up for a week or two later, when the mammary secretion has all the properties and composition of normal milk.

The fluid which is obtained from the breasts on the first two or three days after parturition is called colostrum. It is produced in only small quantities. The yellow colour is due to fat globules (which, if the fluid is permitted to stand, form a layer on the top) along with multinucleated cells loaded with fat particles and known as colostrum corpuscles. These cells are probably phagocytes which have made their way into the mammary alveoli, but some may be desquamated epithelial cells. Colostrum is similar to milk in composition, but contains little or no caseinogen, which is the chief protein of milk, and in the presence of the rennet ferment of the stomach, together with lime salts, becomes converted into the insoluble casein or curd of milk. (The curd also contains the fat globules which are enclosed in its meshes.)

Two other proteins are also present in milk—lactalbumen and lactoglobulin. The sugar in the milk is lactose. In addition to the fat globules, which are held in suspension, the milk contains various salts, such as calcium, sodium, and potassium as chlorides and phosphates. Broadly speaking, the milk of each species contains all those constituents which are necessary for nourishing and supporting the growing young. Thus Bunge has shown that the proportion of inorganic salts present in milk, while differing from those found in the blood plasma, are almost identical with those occurring in the new-born animal,

As mentioned already, a woman does not secrete true milk until the second or third day after parturition. It is produced at that time even though suckling does not take place, as when the child has been born dead. It is necessary, however, in man as well as in animals that the milk should be drawn off in order to maintain the supply, and as is well known, a cow that is not either sucked or milked soon runs dry. The quantity of milk secreted by a woman at first undergoes some increase in accordance with the needs of the child, but after about the twenty-eighth week it begins to fall off, and after about a year the supply ceases. Any longer period involves what is known as *hyperlactation*, a practice which is generally deprecated in the interests of the infant. Menstruation not infrequently commences to occur during the lactation period (according to Fordyce in 40 per cent. cases), and the latter may overlap gestation until within a short time of delivery. The same is true approximately also for the cow, in which animal, in the absence of a new pregnancy, lactation may extend over a very long time.

After the end of lactation the mammary glands gradually return to the size they possessed before gestation, but not to their prepuberal size. The cells lining the alveoli become vacuolated and reduced in number, and as the process of involution proceeds many of the alveoli themselves disappear after first becoming functionless.

In the lower mammals (bitches, etc.) a fluid having all the essential ingredients of milk is secreted some time after the œstrous periods, even in virgins, provided that the mammary tissue is sufficiently built up to admit of its functional activity. This phenomenon, however, only appears to occur normally in animals which ovulate spontaneously, so that corpora lutea "spuria" can be formed, for, as will be shown in the next chapter, mammary growth is mainly dependent upon the functional activity of the corpus luteum. This organ is believed to be an essential factor in the hypertrophy of the glands, but it undergoes involution in the last part of pregnancy, and after parturition the anabolic (or building up) processes no longer predominate in the mammary tissue, the cells of the secretory alveoli undergoing catabolic (or breaking down) changes, which manifest themselves in the active production of milk. Mammary secretion may continue for very prolonged periods after the removal of the ovaries, and

it is said that with castrated cows and goats lactation may continue almost indefinitely, but this is not established. It is noteworthy that there are no secretory nerves supplying the mammary glands, which are therefore in this respect unlike the salivary glands or sweat glands.

The mammary glands of new-born animals sometimes secrete small quantities of what is known as "witch's milk." This fluid contains most of the constituents of normal milk, but the solid substances are less in amount.

In all mammals, with the possible exception of the Monotremata (platypus, etc.), the milk glands are probably of the nature of modified sebaceous glands.

Parturition in the Lower Mammals

The process of parturition in the lower mammals is essentially similar to what it is in man. Its duration varies in the different species. In the mare it takes from five to fifteen minutes, in the cow about two hours, in the sheep fifteen minutes for each lamb born, in the sow, bitch and cat from ten to thirty minutes with sometimes an interval of one hour between each birth. In the Carnivora, the mother usually gnaws through the umbilical cord, but in the other animals it is torn. The placenta may not be got rid of until several hours after the young is born (as in the mare).

Sometimes, as not infrequently happens in the mare, the young animal is born within the intact membranes, and should be liberated in order to avoid asphyxiation, but more usually a few minutes or more elapse before the placenta is detached and got rid of. Occasionally the membranes are retained in the uterus, where they are liable to become infected with bacteria and set up inflammation; if they are not discharged steps should be taken to remove them.

CHAPTER VI

THE INTERNAL SECRETIONS OF THE ORGANS OF REPRODUCTION

We may now consider another rôle played by the essential organs of reproduction, namely, that of elaborating chemical substances and secreting them, not externally by ducts or canals, but internally into the blood, where they are carried throughout the whole body and act both on the general metabolism and on a number of organs and structures which are thereby stimulated in a variety of ways. The earliest evidence that the testes and ovaries act in such a manner was that derived from the effects of castration, an operation practised upon man and also upon the domestic animals from primitive times. The results of testicular and ovarian deprivation are referred to many times in the works of Aristotle, but there is little doubt that the operation was practised before the dawn of history. The purpose of castration as applied to man was to obtain de-sexed individuals or eunuchs, usually for attendance upon women, as is still done in oriental countries. With animals, the operation was carried out for economic purposes, as it is to-day, it having been long recognised that castrated animals fatten faster and more readily, besides being more docile and easier to manage than entire ones. For a similar reason ovariotomy or the removal of the ovaries (the term castration being often restricted to the operation of extirpation of the testes) was practised in quite early times on sows, as recorded by Aristotle, but was not usually done on other animals owing no doubt chiefly to the greater difficulty of performing it.

The general effect of castration in all vertebrate animals is to prevent the development of the secondary sexual characters, that is, of those characters which, while correlated with the sex in question, are not directly concerned with the reproductive processes. This statement applies to ovariotomy as well as

to castration of the male, but it is by no means true of all invertebrate animals, since in insects, for example, removal of the gonads in the immature individual has no effect on the future development of the characteristic secondary sexual characters, a castrated caterpillar changing into a perfect insect, normal in every way excepting for the absence of the generative glands. With vertebrates the castration effects on the secondary characters are usually only brought about if the operation is done prior to puberty or the age when sexual maturity is reached.

Castration in Males

In man early castration arrests the enlargement of the larynx and the consequent deepening of the voice, a fact which was formerly taken advantage of in order to provide "sopranists," as in the case of the choir of St Peter's at Rome. Castration likewise prevents the growth of hair on the face and the other parts of the body which are usually provided with hair in the adult male. The general effect is to produce a superficial appearance of femininity, which is in reality a condition in which certain of the male characters are absent rather than one in which female characters have been acquired. Moreover, castration is followed by atrophy of the prostate and other accessory male glands, or if the operation is carried out before puberty, these do not fully develop, and penile erection does not occur.

There is a disposition towards giantism among eunuchs, since early castration arrests the ossification of the epiphyses[1] of the limb bones, the consequence being that the zones of proliferation persist for a longer time and the bones continue to grow, just as happens also in some cases of pituitary disease. The pelvis of the eunuch tends to maintain the juvenile type. There is often a tendency to put on fat, and Lipschütz refers to the fat, slippery face of the Skopecs, a fanatical tribe in Siberia, who practised castration for religious purposes.

The psychological effects of castration are no less marked. If done before puberty, sexual desire is absent, and if done

[1] The epiphyses are the end portions of the bones which ossify from separate centres in portions distinct from the shafts or main parts of the bones.

subsequently the impulse is lessened, though not always entirely absent. According to Hikmet and Regnault the eunuchs of Constantinople have the following mental characteristics: They are avaricious, illogical, and obstinate (*i.e.* they cannot change or adjust their ideas), they have no capacity for judgment and accept information freely in the absence of proof; they are not cruel, but are fond of children and animals; they are faithful in their affections, but possess no courage; their mental activity is very slight, and they are extremely fanatical. Senility occurs prematurely.

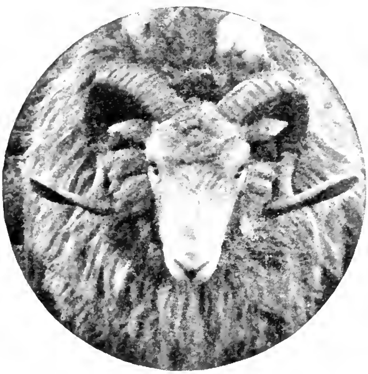


FIG. 56.—Herdwick ram (normal). (From Marshall and Hammond, *Jour. of Physiol.*)

FIG. 57.—Herdwick wether (castrated young). (From Marshall and Hammond, *Jour. of Physiol.*)

With other vertebrate animals the general physiological effects of castration are similar. The ossification of the epiphyses is arrested. The thymus gland which normally atrophies at or about puberty persists longer or even undergoes hypertrophy. The accessory sexual glands tend to atrophy or do not fully develop, according to the time at which castration is done. If performed early penile erection cannot take place, not even on experimentally stimulating the nervi erigentes (dogs). In animals with a seasonal rut, castration prevents the periodic enlargement of the prostate and other glands (hedgehogs, etc.). The secondary male characters, with a few possible exceptions, do not develop. For example, in breeds of sheep which are horned in the male, but hornless in the female (Merino, Herdwick or Welsh), castration arrests the development of the horns,

and it is noteworthy that this happens at whatever stage of growth the operation is performed, the horns ceasing to grow forthwith. It is clear, therefore, that the testicular stimulus is essential, not only for the initiation of horn growth, but also for its continuance and completion. In other horned breeds of sheep (*e.g.* Dorset Horns, Scottish Blackfaced or Lonks) the wethers have horns which are finer and less massive than those of the rams and so approximate towards the horns of the female (or more probably what is really the neutral) type. With deer

FIG. 58.—Herdwick wether castrated when four months old. The horns are the same length as they were at the time of castration. (From Marshall and Hammond, *Jour. of Physiol.*)

FIG. 59.—Herdwick ram lamb from which one testis was removed four months after birth. The horns continued to grow and were symmetrical. (From Marshall and Hammond, *Jour. of Physiol.*)

early castration prevents the development of the antlers. If the operation is performed late, only "clump" or "peruke" antlers, which are quite short, appear, and these persist instead of falling off after the breeding season, as normal antlers do. If castration is done when the antlers have grown, these fall off and are replaced next season by peruke antlers. The horn sheath, however, is not shed. Speaking generally, with all ungulate mammals that are sexually differentiated in respect of horn growth, castration leads to a condition resembling that existing in the female, which in these animals approaches more closely to the neutral type than does the entire male. In the eland, which like many horned sheep, is horned in both sexes,

castration is not followed by the suppression of the horns. In the castrated cat the growth of the tissues of the cheek or jowl is partially arrested. And similarly with other castrated mammals, there is an approach to what appears to be the female or neutral type, both in the general bodily conformation and in the secondary sexual characters.

Castration has been practised on the domestic animals from very early times for economic reasons, as it was recognised that in this condition they fattened better and faster and that working animals (horses, oxen) were easier to manage and generally more serviceable. It is not quite clear whether the tendency to put on fat in castrated animals (a tendency which we find

FIG. 60.—Successive stages in the regression of the comb of the cock after castration : (*a*) at the time of castration ; (*b*) five weeks after ; (*c*) seven weeks after ; (*d*) when regression was complete. (From Pézard.)

also in females which have been spayed, and in women after the menopause) is an indirect effect, due to greater lethargy and freedom from sexual excitement, or whether it is a direct metabolic result of the absence of the sexual glands, but certain investigators (Loewy and Richter, Murlin and Bailey) have found a definite lowering of the metabolism after castration, and it has been suggested that the gonads produce a specific substance which promotes oxidation in the body.

With birds, the effects of castration in the male on the general superficial characteristics is not so striking as with mammals. This may be partly accounted for by the assumption that the neutral type is nearer the female than the male, for, as we shall see later, the removal of the ovary in the female results in the development of what one is accustomed to think of as male characters. With fowls, castration is followed by an arrest in

the development of the erectile structures about the head (comb, wattles, etc.). The general plumage, on the other hand, is as characteristically male in the capon as in the cock, and the spurs also are unaffected. So also the castrated drake differs only slightly from the uncastrated male bird (Goodale, Pézard).

With the frog, castration inhibits the development of the clasping pad at the base of the forefinger at the breeding season, as well as the associated hypertrophy of the musculature of the fore limb. With other amphibians and also with fishes, the appearance of certain secondary male characters has been shown to be correlated either with the testis or with a special organ usually in contiguity with the testis. With all the higher vertebrates, however (birds and mammals), it is abundantly evident that the secondary sexual characters in the male are dependent upon the presence, and consequently upon the functional activity, of the testis itself.

The Internal Secretion of the Testis

The idea that the testis exerted its influence upon the secondary sexual characters or upon the metabolism through an internal secretion discharged into the blood rather than through the intermediation of the nervous system, seems to have been first postulated by Bordeu, who was Court Physician to Louis XV. of France in the eighteenth century. It was not, however, until 1849 that the conception came to be based upon definite scientific evidence, for it was in that year Berthold published the results of his experiments upon testicular transplantation in fowls. Berthold's views and work were for many years lost sight of, but it is remarkable to note that some of the strongest and clearest evidence that the testis elaborates one or more chemical products which are secreted internally and carried through the circulation, is that derived from experiments with testicular grafts, carried out in a manner essentially similar to that employed by Berthold. That the gonad (whether male or female) when removed from the normal position and transplanted on to an abnormal position (such as the ventral peritoneum), where it no longer possesses its ordinary nerve connections, yet still retains its usual influence on the secondary sexual characters and even upon the accessory sexual glands, is only explicable on the assumption that it secretes

chemical substances or hormones internally into the blood, and that these act upon other and sometimes distant organs in the body. In the experiments upon fowls the testes were removed and sometimes broken up into numerous pieces, and these grafted themselves on to the different parts of the peritoneum or on to the outside wall of the gut, and the birds developed typical male characters (growth of comb, wattle, etc., male voice, and sexual and combative instincts). Such birds were not capons but typical cocks, excepting that they were unable to fertilise the eggs in treading the hen (Foges, Shattock and Seligman, etc.). So also with the frog, Nussbaum showed that if the testes were removed and one of them grafted into the dorsal lymph sac, the musculature of the forearm underwent the usual hypertrophy, and the clasping pad at the base of the second digit duly developed at the onset of the breeding season. Experiments upon rats have shown that if the testes be removed and grafted on to the peritoneum or abdominal muscles, the prostate gland, vesiculæ seminales, and penis develop normally; and similarly with other animals. Moreover, the experiments of Steinach, Moore, Sand, and others have shown that the transplantation of testes from other individuals may promote the development of secondary male characters in animals which were congenitally females, and so the sex of the individual may be partially or almost completely reversed. There are a large number of other experiments with testicular grafts, which afford confirmatory evidence of what is now regarded as an established fact that the testis and (as we shall show later) the ovary are organs producing internal secretions, and exert their influence through the intermediation of the circulatory system.

It is, of course, arguable that centripetal nerve fibres grow into the grafted gonad, and that in this way a new path is established leading to the central nervous system, but it would seem very unlikely that such a connection could be formed by an organ in a quite abnormal position in the body. Injection experiments, however, are not open to this criticism, but it must be admitted that the evidence derived from these is still somewhat inconclusive. Among the most satisfactory experiments are those of Ancel and Bouin, who injected testicular extract subcutaneously into castrated guinea-pigs over a period of nine months, and found that the penis and vesiculæ seminales

were much more fully developed than in castrated control animals. More recently Pézard made intraperitoneal injections of pigs' testes into a capon, and induced a growth of the comb and other erectile structures on the head. The fact that one-sided castration produces no effect on the symmetry of the secondary sexual characters (*e.g.* the horns of the Herdwick ram) or upon the development of the accessory generative glands (*e.g.* the vesiculæ and prostate in the hedgehog) is further evidence that the gonads act through hormones circulating in the blood rather than locally through the nervous system.

The question as to the seat of production of the testicular hormone is not yet definitely solved, but in mammals at least it is widely believed that it is elaborated by the interstitial cells rather than by the spermatogenetic tissue or other cells belonging to the tubules. The evidence on which this conclusion is based is derived from the study of cryptorchid or undescended testicles in which no spermatogenetic tissue is present, and from vasectomy and x-ray experiments, and from grafts in which the interstitial tissue only appeared to have been functionally active.

Thus in Tandler and Gross's investigation on the roe-buck, the animal's testes were subjected to the x-rays, and as a consequence all the spermatozoa and spermatogenetic cells were destroyed, but the interstitial tissue remained unaffected. In the breeding season the horns grew in an entirely normal manner, and so distinguished the "Röntgen buck" from the castrated buck in which the horns did not undergo the usual periodic development. Bouin and Ancel were the first to show that when the vasa deferentia in the horse and other animals are ligatured or cut, although the spermatogenetic tissue of the testis ceases to be functional and gradually undergoes atrophy, the interstitial cells do not atrophy. Indeed, it is affirmed by Steinach and others that under these conditions the interstitial cells even hypertrophy. This result is not clearly understood, but it may be that tubules degenerate owing to their contents being unable to escape, and that consequently the intervening cells are provided with space to hypertrophy associated with an increased vascularisation. Moreover, as Copeman also showed, under the conditions of such experiments, the presence of the interstitial cells only, suffices for the development of the secondary sexual

characters. In consequence of this function Bouin and Ancel designated the tissue in question the "interstitial gland," and Steinach subsequently called it the "puberty gland," in view of the great acceleration in all the sexual processes, and in the correlated growth of the secondary characters, at the period of puberty, in association with the development of this gland. Furthermore, cases of testicular transplantation in man are recorded by Lichtenstern and others who have claimed cures for eunuchoidism and homosexuality as well as for debility and impotence, and in certain of these it is apparent that of the testicular elements which remained in the grafts, the interstitial cells alone possessed any functional capacity. The same is true in the case of Thorek's grafts of chimpanzee's testis upon man, the histological preparations made subsequently showing that the interstitial elements had proliferated, whereas the tubules had undergone atrophy. According to Voronoff, on the other hand, the hormone produced by the "monkey gland" comes from the epithelial cells.

It is, however, a very open question whether the interstitial tissue in birds' testes elaborates the hormone, for in this class the cells outside the tubules are rarely epithelioid, many of them at any rate being of the nature of ordinary connective tissue cells. Nevertheless, some observers (Massaglia, etc.) attribute the hormone-producing function to the interstitial tissue in birds as well as in mammals.

Ovariotomy

The effects of removal of the ovaries are, in a general way, of a similar kind to those following castration in the male. If the operation be done before puberty, the uterus remains infantile and the mammary glands fail to develop. If done after puberty the uterus degenerates, the mucous membrane undergoing fibrosis, the lumen becoming reduced in size, while the glands and muscles atrophy. In regard to the effect of ovariotomy on the secondary sexual characters, the tendency is to produce a neutral type similar to that of the castrated male, at least in the higher vertebrates. Thus the shape of the head in the castrated cow is like that of the ox (Tandler and Keller), and similarly with the pelvis in the sheep (Franz). Speaking generally,

however, the external changes in mammals are less marked after ovariotomy than after castration of the male, since in this class the female is much nearer the neutral type than the male is, the secondary characters being for the most part positive in the male sex and negative in the female.

In birds, on the other hand, the male is closest to the neutral type, and consequently removal of the ovary (for there is generally

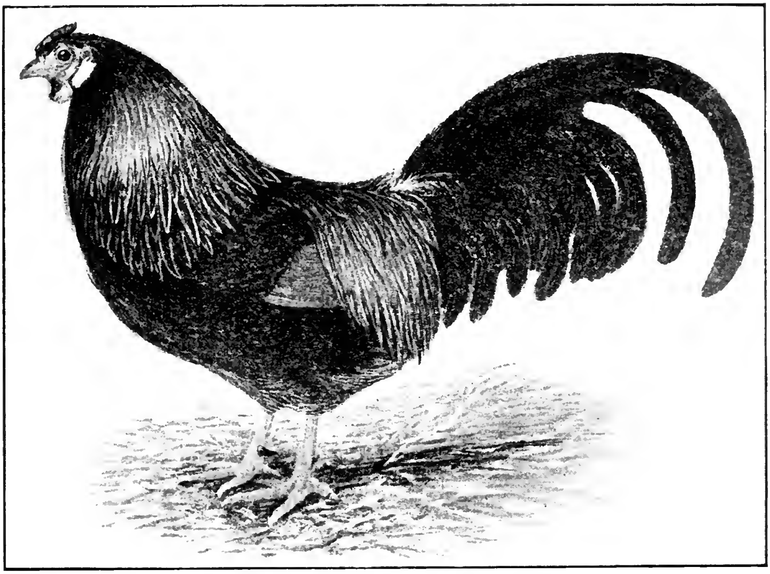


Fig. 61.—Ovariotomised brown Leghorn hen. (From Goodale.) The bird shows male feathering and spurs, but the comb and other erectile structures are not hypertrophied.

only one) leads to an assumption of apparently male plumage, but the more strictly male characteristics are not acquired. Thus ovariotomy in the fowl is followed by the growth of the spurs and the assumption of much of the male feathering (the bird looking at first sight much like a cock), but the comb, hackles, and other erectile structures about the head remain unaffected (Goodale, Pézard, etc.). Similarly the castrated duck, to a great extent, acquires the external characters of the drake (Goodale). The castrated female ostrich also assumes the typical tail feathering of the male, and since this is an economic advantage with

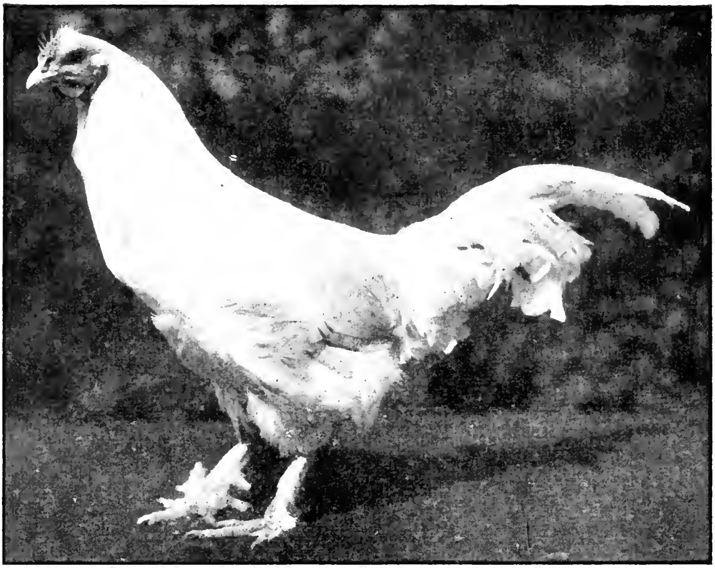


Fig. 62.—Ovariotomised pullet with plumage and spurs of male, *i.e.* of neutral type according to Pézard. (From Pézard.)

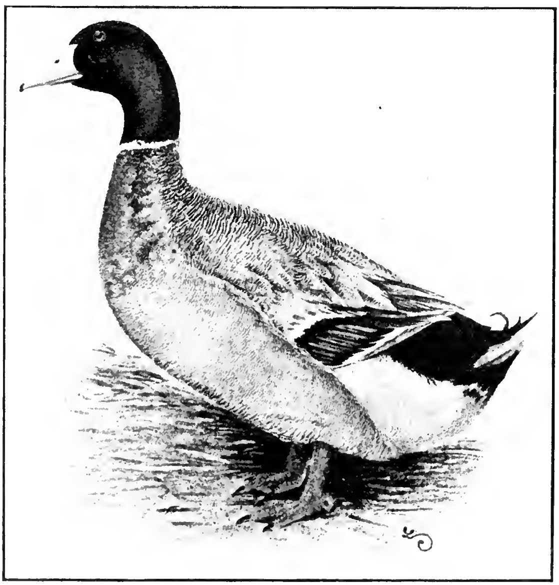


Fig. 63.—Normal Rouen drake. (From Goodale.)

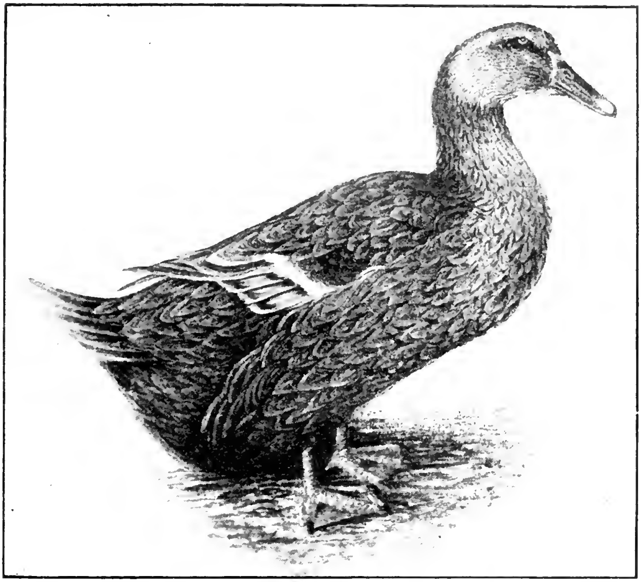


FIG. 64.—Normal Rouen duck. (From Goodale.) (*Cf.* Figs. 63 and 65.)

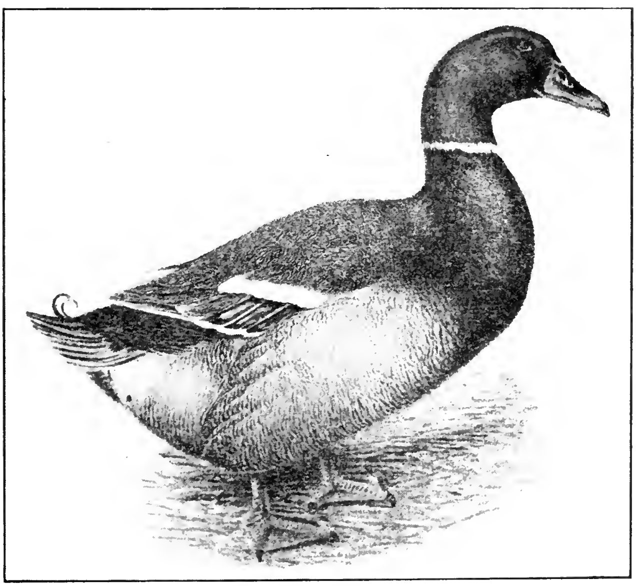


FIG. 65.—Ovariotomised Rouen duck. (From Goodale.) (*Cf.* Figs. 63 and 64). The bird was operated upon when six weeks old.

ostrich breeders in South Africa, the operation is often carried out. It is noteworthy that the castrated male and female ostrich are identical in type.

In insects, however, there is no correlation between the ovaries and the external female characters any more than between the testes and characters of the male.

Ovariotomy in women prevents the recurrence of menstruation, or if done before puberty, the menstrual cycle never begins. Similarly with other mammals, the œstrous cycle does not recur in the absence of the ovaries. The removal of the uterus (hysterectomy) without the ovaries, on the other hand, does not inhibit œstrus, and the ovaries continue to produce ova and to form corpora lutea, the mammary gland also undergoing cyclical changes. Ovariotomy is sometimes performed on the domestic animals for economic purposes, but not so commonly as castration in the male. In the sow it is done to promote fattening, the pigs feeding better and more regularly, being undisturbed by sexual excitement at the three-weekly periods when œstrus would otherwise occur. Ovariotomy is also done occasionally on vicious or troublesome mares which become unworkable at the œstrous periods especially in the presence of stallions.

As already remarked in discussing castration, there is some evidence that the removal of the gonads induces fattening by causing a reduction in the metabolism, this having been shown by Murlin and Bailey in the case of bitches. A tendency towards adiposity is sometimes well marked after the menopause or climacteric when there are also other indications of the decline of ovarian influence, as manifested in the assumption of male (or at any rate neutral) secondary sexual characters (*e.g.* the tendency to grow hair on the upper lip and chin in elderly women).

The Internal Secretions of the Ovary

The evidence that the ovary is an organ of internal secretion is of similar kind to that showing that the testis is such an organ. If the ovaries, instead of being entirely removed, are grafted (or only one is grafted) in an abnormal position, such as the ventral peritoneum or the interior of the kidney, in spite of the fact that the ordinary nerve connections are severed, the uterus, instead of undergoing atrophy, is maintained in its normal

condition. Moreover, the œstrous cycle continues. Similarly menstruation may continue after the attachment of a successful ovarian graft in women otherwise deprived of their ovaries. Both with man and animals the graft may be from another individual, but transplantation is more difficult to effect in such a case, although seemingly favoured by close blood relationship. Experiments with injection of ovarian extract are less satisfactory, but in a number of instances, congestion of the uterus and other indications of heat or œstrus have been brought about both with spayed animals and also with anœstrous ones, which had not been deprived of their ovaries. (See p. 101.)

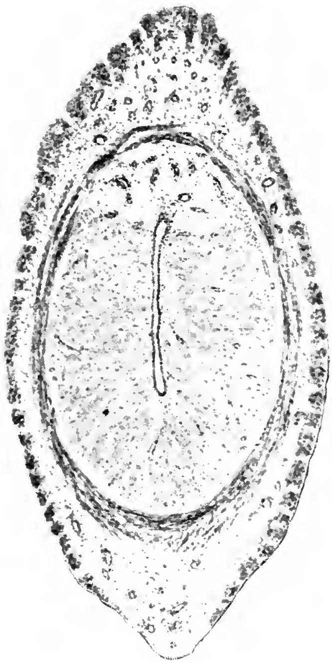


Fig. 66.—Transverse section through uterus of rat after ovariotomy, showing degenerative changes. (*Cf.* Fig. 20.) (From Marshall and Jolly.)

The Interstitial Cells.—As just mentioned, there is an undoubted functional correlation between the ovaries and the normal nutritional condition of the uterus. Furthermore, there is evidence that the ovarian elements responsible for maintaining this condition are the interstitial cells, for M'Ilroy and others have shown that the normal condition is preserved by ovarian grafts in which the follicle cells have degenerated, and of the possible secretory elements only the interstitial cells remain. The study of the distribution and comparative physiology of the interstitial cells is still, however, very imperfect, and in some animals these elements have not been discovered, at any rate, in the ovaries of the adult. It is not unlikely that there is considerable variation among the different species of mammals in regard to the development and functional importance of the interstitial cells, and it is possible that they are potentially equivalent to the follicular epithelial cells, since certain

investigators state that they have an identical origin with the latter, both being derived from the primitive germinal epithelium and not from the connective tissue. The stimulus for the

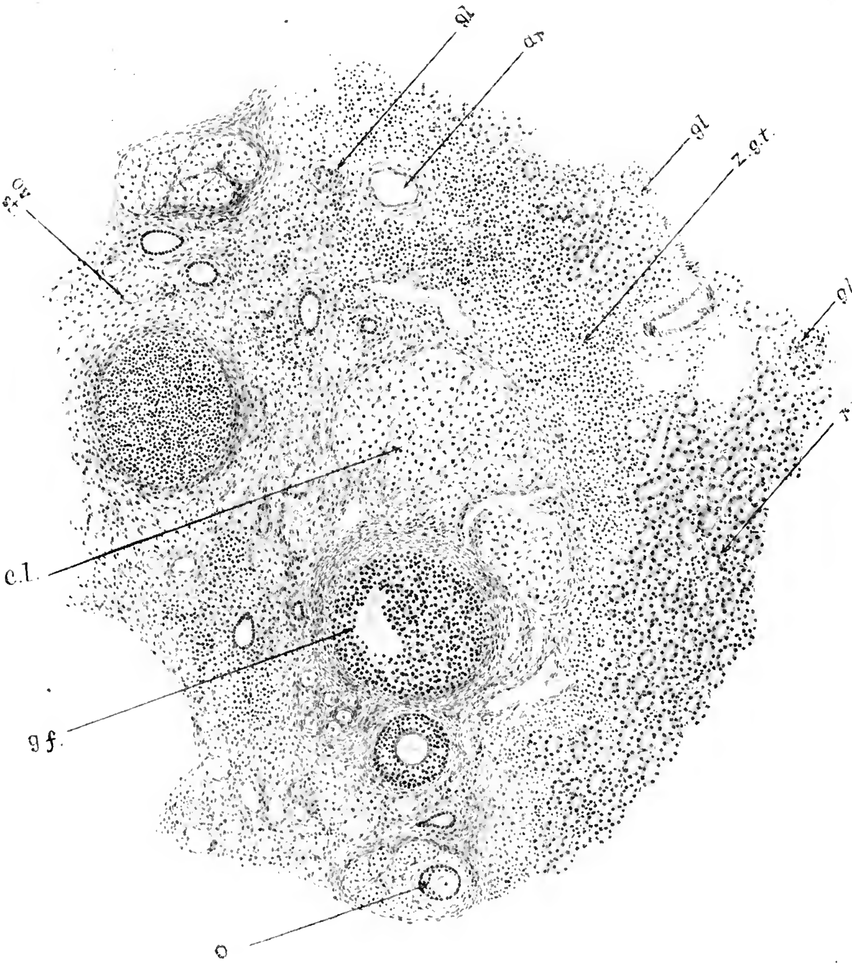


FIG. 67.—Section through rat's kidney, into the tissue of which an ovary had been transplanted. (From Marshall and Jolly, *Quar. Jour. of Experimental Physiology.*)

ar Artery; *c.l.*, corpus luteum; *g.f.*, Graafian follicle; *gl.*, glomerulus of kidney; *ov.st.*, ovarian stroma; *r.t.*, renal tubule; *z.g.t.*, zone of granulation tissue between ovarian tissue and tissue of kidney.

development of the secondary sexual characters has also been referred to the interstitial cells, and, as we shall see later, the early sex differences even in the fœtal stage of development are sometimes accounted for by reference to an embryonic interstitial gland.

The Cause of Heat.—Recent experimental and observational evidence points to the conclusion that "heat" in mammals is directly correlated with the secretory activity of the epithelial cells of the ripe Graafian follicle. Thus Robinson states that in the ferret œstrus is experienced only when the follicles are in a state of ripeness which he calls the pre-enseminal stage, and that this stage may be very prolonged if copulation does not occur. Hammond has made observations on the rabbit, showing that an extended heat period is associated with an œstrus of indefinite length. Moreover, in the dog it has been found that if the follicles approaching maturity are destroyed experimentally, heat does not supervene at the expected time, but may recur subsequently in association with a new batch of ripe follicles (Marshall and Wood). Furthermore, Allen and D'Oisy state that they can induce heat in rats after the removal of the ovaries by injecting specially prepared alcoholic extracts of liquor folliculi, and this has been confirmed by Courrier on the guinea-pig and hedgehog. There is, moreover, some evidence that where there is persistent œstrus (nymphomania) associated with the presence of ovarian cysts, as with cows and occasionally with women, this abnormal condition is correlated with hyperactivity on the part of the epithelial elements of the ovary.

The Functions of the Corpus Luteum.—The main part played by the corpus luteum is now beyond the reach of controversy. Broadly speaking, this organ is responsible for the changes which take place in the accessory female generative organs and mammary glands during pregnancy and pseudo-pregnancy.

To Fraenkel belongs the credit of assigning to this organ a definite rôle as an internally secreting organ, and basing his view on experimental evidence. According to this investigator, the corpus luteum had the function of elaborating a hormone which in some way assisted in the attachment of the fertilised ovum to the uterine mucous membrane, and in the maintenance of its nutrition in the first part of pregnancy. The evidence, which has been repeatedly confirmed, was derived mainly from

the results of experiments on rabbits, in which the ovaries were removed or the corpora lutea destroyed by the electric cautery, and in each case pregnancy was brought to an end. Control experiments showed that the results were not simply post-operative. It is, however, hardly justifiable to regard the corpus luteum as the responsible factor in the attachment or nutrition of the ovum or early embryo in any other sense than

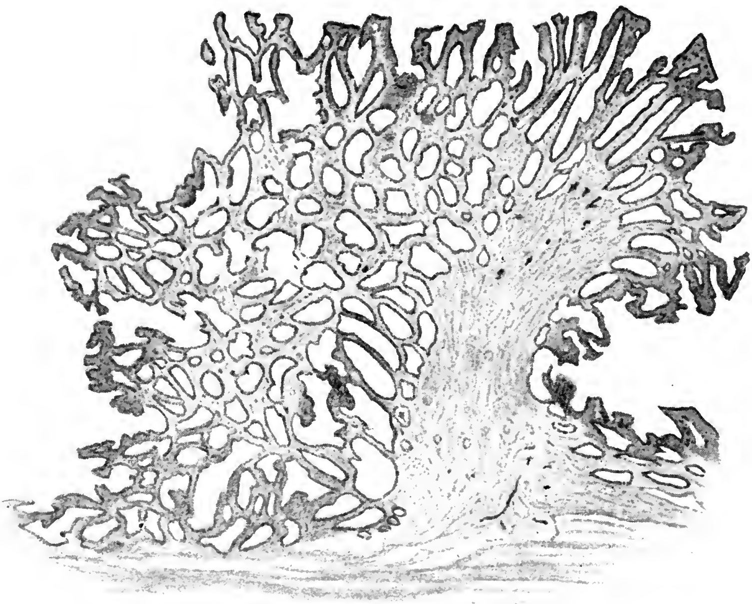


FIG. 68.—Section through uterine mucosa of rabbit nine days after sterile coition. The condition is one of pseudo-pregnancy, the glands being very well developed. (From Hammond and Marshall.)

that implied in stating that this organ, through the secretion it produces, acts as a stimulus to the growth of the uterine mucosa and the maintenance of the increased uterine nutrition which are necessary for the occurrence of gestation. This latter view as to the function of the corpus luteum was first placed on a completely firm foundation by Ancel and Bouin who showed that the organ exerts a comparable influence on the rabbit's uterus in pseudo-pregnancy, a condition which occurs only after sterile coition (as with a vasectomised buck). Since the rabbit does

not ovulate except after copulation it follows that under normal conditions corpora lutea are associated with pregnancy, and that

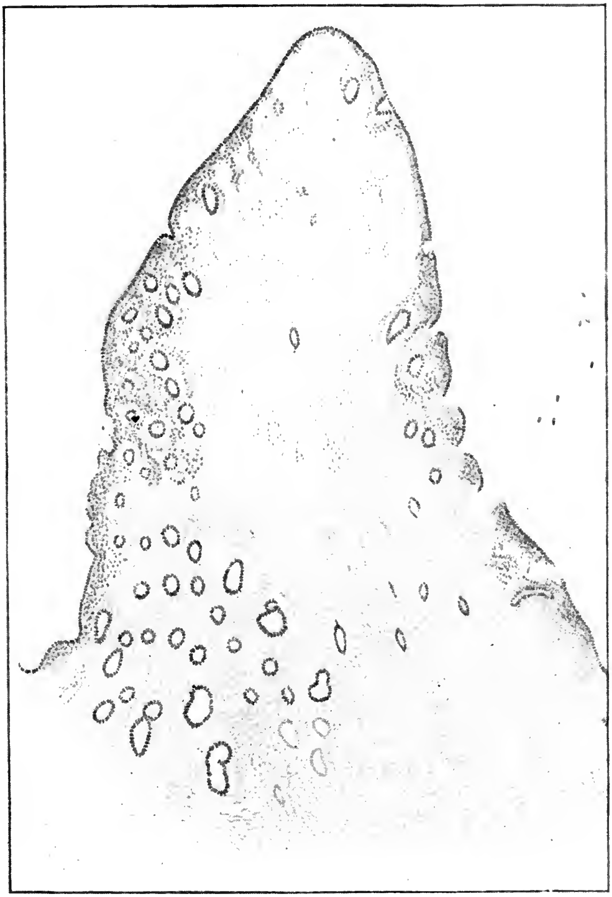


FIG. 69.—Section through uterine mucosa of rabbit twenty-four days after sterile coition (retrogressive stage in pseudo-pregnancy). A great quantity of extravasated blood is seen. The glands are still somewhat enlarged. (From Hammond and Marshall.)

the so-called "corpus luteum spurium" (which in other animals is formed after a spontaneous ovulation) does not exist. If, however, a doe rabbit is induced to ovulate under such experimental conditions that gestation cannot supervene, the development

of the corpora lutea is correlated with pronounced uterine and mammary hypertrophy in the manner already described as constituting pseudo-pregnancy. There can be no doubt that these changes are essentially similar to those which take place in true pregnancy, and consequently that the corpus luteum is the organ which is responsible for these changes in normal gestation.

That the ovary with its contained corpus luteum may be removed in the latter part of pregnancy in women, as well as in some animals, without causing abortion, is explained by Fraenkel as due to the corpus luteum being in a state of commencing involution and no longer functional, the uterine mucosa being already sufficiently built up to admit of fœtal nutrition being maintained. The effect of ovariotomy late in pregnancy upon the mammary glands, however, is still uncertain, but Hammond has shown that in the rabbit the growth of the mammary glands is under the influence of the corpus luteum throughout the whole of gestation.

In the virgin rabbit the mammæ are limited to a few ducts in the immediate neighbourhood of the nipple, but as soon as the corpus luteum is formed hypertrophy sets in. The mammary glands of pseudo-pregnancy (which in this animal only occurs under experimental conditions after a sterile copulation) do not develop to the same extent as with true pregnancy. It is to be noted that in the marsupial cat (Hill and O'Donoghue) and the opossum (Hartman) as well as in the bitch (Marshall and Halman) the uterus and mammary glands undergo hypertrophy during pseudo-pregnancy in the same kind of way, but usually to a less degree than they do during gestation; milk secretion, however, generally follows. Thus, even in virgin bitches milk is frequently secreted at the close of pseudo-pregnancy when the corpora lutea are undergoing involution, and many instances are recorded of such animals suckling litters of pups produced by other individuals (Heape, Paton, Blair Bell, etc.). In these animals which ovulate spontaneously pseudo-pregnancy may be regarded as a normal state if the ova are not fertilised at œstrus, and the series of changes is to be regarded as homologous under the two conditions, the difference being that in the absence of true pregnancy the development of the uterus and mammæ is futile, owing to the absence of an embryo. In polyœstrous animals,

such as the sow, the diœstrous interval is occupied by what may be considered as an abbreviated pseudo-pregnancy (*cf.* Corner), brought about under the influence of the corpus luteum "spurium," which very shortly undergoes involution in prepara-

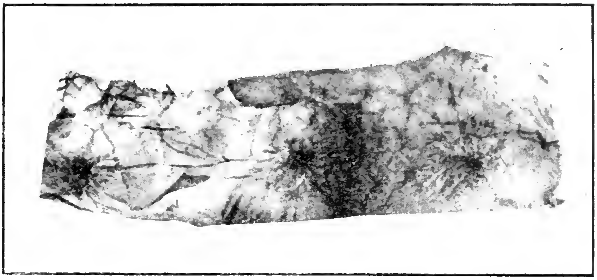


FIG. 70.—Photograph of mammary tissue of virgin rabbit. The mammary development is limited to a few ducts. (From Hammond and Marshall.)

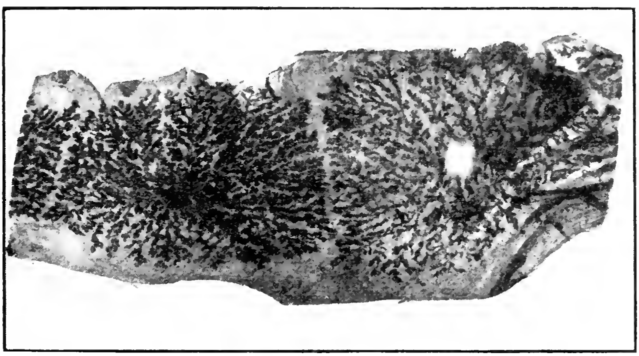


FIG. 71.—Photograph of mammary glands of pseudo-pregnant rabbit fourteen days after œstrus. The rabbit had never bred. (From Hammond and Marshall.)

tion for the maturation of a new batch of follicles and a new heat period. In the heifer also, as Hammond and Woodman have shown, the mammary glands may be sufficiently built up to result in secretory activity, a fluid containing all the constituents of milk being produced even in the virgin animal (Asdell). In women, as in the pseudo-pregnant lower mammal, there is a post-œstrous uterine hypertrophy, with great glandular development,

and the premenstrual uterus is said to undergo changes similar to those of the pregnant organ, and it is probable that these also depend upon the corpus luteum. Corner has described comparable changes in monkeys, but only if ovulation had occurred previously.

Decidual cells are not normally formed in the uterine mucosa excepting in true pregnancy, but as was first shown by Leo Loeb in the guinea-pig, nodules composed of decidual tissue can be induced to develop as a result of direct stimuli to the mucosa, such as the introduction of a foreign body or the making of incisions in the mucosa. The nodules which Loeb describes under the term "deciduomata" arise through the proliferation of the inter-glandular connective tissue. They can be induced to form most readily from the third or fourth to the eighth or ninth days after heat, and therefore at a time when freshly formed and active corpora lutea are present in the ovaries. The formation of decidual tissue was not caused by ova in the uterus, since it took place when that organ was ligatured off so as to prevent the passage of the ova. If, however, the ovaries with their contained corpora lutea are extirpated, deciduomata are not produced. On the other hand, if pieces of uterine mucosa are transplanted into subcutaneous tissue decidual nodules are formed in the grafted tissue. Loeb concludes, therefore, that for a certain interval after ovulation the corpora lutea elaborate a predisposing substance in the presence of which indifferent stimuli may produce the formation of deciduomata.

Hammond has shown further that placental tissue may be formed in the uterine mucosa of the rabbit by similar methods, but only during an experimentally induced pseudo-pregnancy. Such a formation of decidual tissue is clearly comparable to that produced during true pregnancy when corpora lutea are normally present in the ovaries.

Long and Evans state that in the rat, owing to the short "diœstrum" and the corresponding abbreviation in the duration of the "corpus luteum spurium" or "corpus luteum of ovulation," deciduomata cannot be induced in the uterine mucosa. If, however, the female rat undergoes a sterile coition with a vasectomised male the corpus luteum persists for a longer period and the subsequent œstrus is postponed. This is believed to be due to the formation of the vaginal plug which extends into

the cervical canal of the uterus and has a direct stimulating effect on the mucosa, producing a condition of pseudo-pregnancy, and the corpus luteum itself persists for a longer period. The same result can be brought about in the absence of the male by

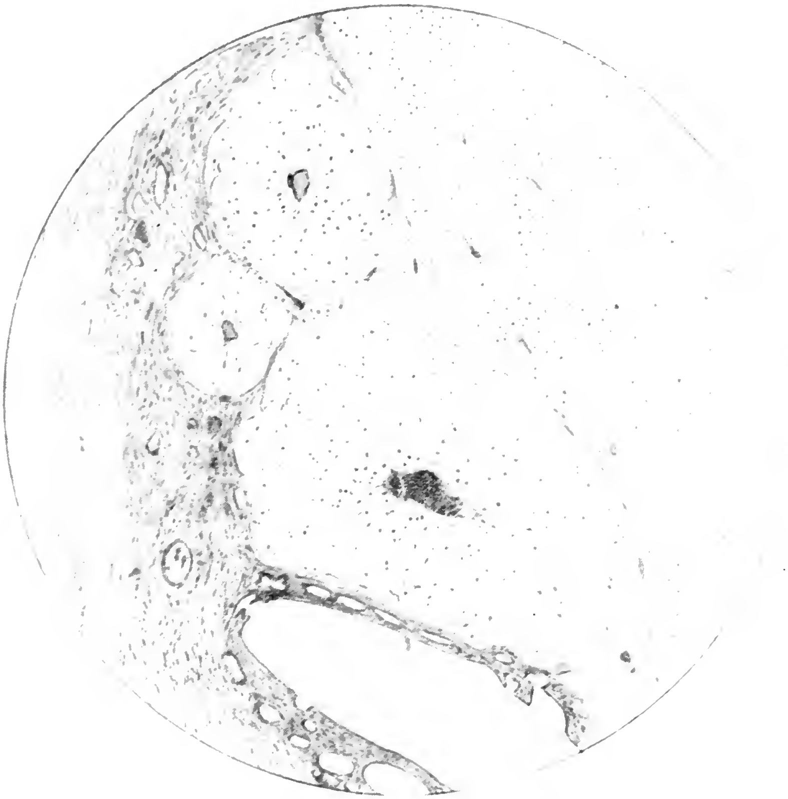


FIG. 72.—Experimentally produced placenta of pseudo-pregnant rabbit; section of uterus showing connective tissue forming decidual cells which enclose vessels. (From Hammond.)

mechanical stimulation of the tissues at the anterior end of the cervix by a tube or glass rod. Further, if during pseudo-pregnancy the uterine mucosa were subjected to irritation induced by injury or by the introduction of fine threads into the uterine cavity, deciduomata were formed in just the same kind of way as with the guinea-pig or the rabbit. It is believed,

therefore, that the internal secretion of the persistent corpus luteum sensitises the uterine mucous membrane, thereby rendering it capable of reacting to mechanical stimulation in the rat, just as it has been shown to do in the other animals experimented upon. In the pregnant animal in which the corpus luteum also persists the direct stimulus is produced by the fertilised ovum.

It has been already mentioned that in polyœstrous animals the corpus luteum spurium persists for only a short time. This, to speak teleologically, is to admit of ovulation and heat recurring after a short interval, since these processes cannot normally take place in the presence of a fully functional corpus luteum in either ovary. It would appear that this organ dominates the ovarian metabolism and inhibits the secretion which is a normal factor in producing the procestrum and œstrus. It also arrests the ripening of the follicles. In monœstrous animals like the dog, on the other hand, the corpus luteum persists during a pseudo-pregnant period, since in such animals a new heat is not in any case due until a prolonged interval after the previous ovulation.

Under certain abnormal conditions the corpus luteum of the cow, and so possibly in other animals, may persist for a prolonged period unaccompanied by pregnancy. Such a condition is usually associated with some pathological affection of the uterus or Fallopian tubes, but the affection by itself is often slight and insufficient to cause sterility. The corpus luteum, however, inhibits the occurrence of œstrus, for, as first shown by Zschokke and now confirmed by many others, if the corpus luteum is squeezed out and thereby destroyed (as can be done in the cow through the rectum) œstrus will generally recur within a few days, and the cow may be got to breed. Furthermore, Hammond has shown that if the normal corpus luteum of a cow is pressed out some time during the "diœstrous" interval, a new heat period will ensue several days before the normal time for recurrence. So also with regard to ovulation; Leo Loeb found in the guinea-pig that if the corpora lutea "spuria" are removed from the ovaries, the ovulation interval may be reduced from the normal sixteen or eighteen days to twelve or even six days.

The Ovaries and Parturition.—The study of pseudo-pregnancy in the bitch, the experimental rabbit, and the marsupial cat throws some light on the factors responsible for parturition.

In each of these species there is present at the end of pseudo-pregnancy a persistent corpus luteum in a condition of involution not dissimilar to that of the corpus luteum verum at the end of true pregnancy. Further, pseudo-pregnancy can only occur when a corpus luteum is present. Moreover, all these animals display habits and instincts at the end of pseudo-pregnancy which are identical with or similar to those associated with parturition. Thus the bitch may prepare a bed as if for a litter of pups, the doe rabbit plucks her breast of fur and uses it to line a nest (Hammond), and the female marsupial cat cleans out her pouch as though for the reception of young (Hill and O'Donoghue). It has been shown that the occurrence and duration of pseudo-pregnancy are dependent on the corpus luteum, and consequently it is exceedingly probable that the processes associated with parturition are similarly correlated with changes in the amount or character of the ovarian secretions.

The manner in which the ovary influences the uterine contractions has recently formed the subject of experimental investigation (Dixon and Marshall), and evidence has been adduced to show that it may act through the intermediation of the posterior lobe of the pituitary gland (a small organ lying underneath the third ventricle of the brain). It is well known that extract of this organ promotes uterine contraction, and that it is used practically by obstetricians to expedite labour, especially in cases of difficulty. Owing to its exceptionally powerful effect, pituitary extract must be used with great caution, as it may produce "contraction rings" on the fœtus, which is consequently born dead. It has now been shown that ovarian extract may promote pituitary secretion, as manifested by the effect of the substance obtained by drawing off samples of cerebro-spinal fluid after injecting ovarian extract into the circulation. It had already been shown that the pituitary gland secretes its active principle into the cerebro-spinal canal, whence it passes into the vascular system and is distributed throughout the body. In the experiments referred to, extracts of rabbits' and sows' ovaries were obtained at different periods of pregnancy and of the œstrous cycle, and injected into a dog; samples of the cerebro-spinal fluid were then drawn off from the dog and tested upon guinea-pigs' uteri suspended in Ringer's solution (a saline fluid resembling blood serum), and the degree (if any) of the contraction of the uterus duly observed

and recorded. It was found that of the various substances employed (testis, epididymis, pancreas, corpus luteum, etc.), extract of ovary alone had a positive effect, but only if the ovaries employed did not contain fully formed and presumably active corpora lutea. Ovaries throughout pregnancy gave a uniformly negative result until near the end of the period, when the uterus (acted on through the intermediation of the pituitary) became increasingly excited as the end of the gestation period was approached. The most extensive uterine contractions occurred as a result of employing ovarian extract obtained just about the date when parturition was due. It is suggested, therefore, that the excitatory mechanism of the ovary is inhibited during pregnancy when the corpus luteum dominates the ovarian metabolism, but that as this structure regresses the normal secretion is once more formed in sufficient quantity to produce a stimulus which reaches and passes the threshold, and so, working through the pituitary, brings about those uterine contractions which are the immediate cause of birth. It was found also that extract made from ovaries at the heat periods (when corpora lutea are absent), and utilised in the same manner, likewise promoted uterine contraction, an observation which conforms with the experience that pains resembling those of labour may occur in association with menstruation. Extract of ovary containing developed luteal tissue, whether or not the animal from which it was obtained was pregnant, invariably led to a negative result. These results are at any rate suggestive.

The Gonads and the Other Organs of Internal Secretion.—It is as yet impossible to formulate any general scheme to describe the relation between the gonads and the other organs of internal secretion, and such facts as are definitely known must, for the present, remain isolated. It has just been shown that there is probably some correlation between the ovarian cycle and the activity of the posterior lobe of the pituitary. It has long been recognised that the thyroid gland is very liable to enlargement at menstruation as well as during pregnancy, and that the swelling at the time of puberty may sometimes lead to goitre. It is also stated that the sexual act and marriage, in both sexes, may increase the activity of this gland (M'Carrison). There is also some evidence of a correlation between the suprarenals and the gonads. Thus it is stated that in rabbits the suprarenal cortex

becomes much thicker in pregnancy, while the medulla becomes thinner (Gottschau). The removal of the gonads also influences the other internally secretory organs, and notably the anterior lobe of the pituitary, which enlarges under this condition.

Conversely, lesions or abnormalities in the organs of internal secretion are known to affect the gonads. Thus hyperpituitarism, due to over-activity of the anterior lobe, is often associated with premature sexuality or excessive desire. On the other hand, a lesion in the pituitary may be followed by atrophy of the seminiferous tubules, as in cases of dystrophia adiposogenitalis, where the individual affected becomes abnormally fat as well as sterile (Cramer and Mottram). Removal (or partial removal) of the anterior lobe is followed by hypoplasia of the generative organs, or if the operation is done before puberty by persistent infantilism. After removal of the thyroid glands, generative activity is said to cease, but this result may be due to the general metabolic disturbance.

The relation between the thymus and the gonads is more problematical, but as already said, castration favours persistence of the thymus which otherwise atrophies about puberty.

The view that there is a fœtal organ of internal secretion in the gonad, and that this is the main cause of sex-determination, is referred to in the next chapter.

The Gonads and Rejuvenation

The idea of a connection between testicular or ovarian influence and rejuvenation was put forward by Brown-Séquard about 1889, and formed part of a general theory concerning the metabolic effects of the gonads. The theory was based chiefly upon the supposed beneficial results of injecting extracts of testis and ovary, obtained from animals, into aged men, and although tentatively accepted by some, was soon discredited, as it became evident that the rejuvenating effects claimed were apparent rather than real. What is essentially the same idea has been recently brought into prominence again by Steinach and others, and more especially with reference to the interstitial or " puberty " gland. The grafting of a human testis from one individual to another seems to have been first done by the American surgeon Lespinisse, and Stanley and Kelker,

Voronoff, and others have performed the same operation with various modifications in method (in some instances the grafts being obtained from animals), and satisfactory results have been claimed. Further, the grafting of testicles obtained from apes (the so-called " monkey glands ") has been practised with apparent success by Voronoff and Thorek, and sections of the transplanted organs have subsequently been made, showing that the testicular tissue had, in part at least, been preserved over periods of several months.

According to Steinach, rejuvenation can also be brought about by vasectomy or ligaturing of the vas deferens, operations which result sooner or later in the atrophy of the spermatogenetic tissue without interfering with the interstitial tissue. It is not clearly understood why the spermatogenetic tissue should be destroyed as a consequence of the operation, and the results obtained by various observers are by no means uniform. Thus in testicular grafts in fowls spermatogenesis is known to continue for some time at any rate after the transplanted organ has become attached and without there being any exit for the seminiferous fluid or spermatozoa. There can be no doubt, however, as already mentioned, that vasectomy does frequently, if not usually, result in cessation in the production of the spermatozoa, and sooner or later in the degeneration of the seminiferous tubules. Steinach goes further and states that as a consequence of the changed conditions in the testis the interstitial tissue undergoes hypertrophy, and the resulting rejuvenation of the organism is attributed to this hypertrophy on the part of the puberty gland. The operation has been done upon aged men, both bilaterally and unilaterally, and is stated to have been followed by favourable results. The advantage of the unilateral operation is that one testis remains fully functional. Steinach has also claimed to have obtained successful results in rejuvenating rats by vasectomy, and Sand has recorded similar results with dogs. A number of other surgeons, both European and American, claim to have brought about rejuvenation and other beneficial effects in men, both by vasectomy and by grafting.

A possible fallacy underlying this type of experiment is that the result of any nutritional or environmental influence is not easy to determine and may be neglected, while control experiments are not always easy. Moreover, with operated men it is

generally possible to explain the results as being in part due to suggestion, and it is noteworthy that the benefit obtained is rarely, if ever, maintained for any prolonged period. Nevertheless, it must be admitted that there is now a considerable accumulation of evidence that both vasectomy and testicular transplantation may be followed by general improvement, and this may be interpreted as a rejuvenation.

General Conclusions

The testis is an organ producing an internal secretion which is formed throughout the whole reproductive period of life, and probably earlier, though to a much less extent, and possibly even in the embryo. In those animals which experience rut it is at this season that the testicular hormone is produced in greatest abundance. The periodic development of the prostate and other accessory glands as well as the secondary sexual characters, not to mention the testes themselves, is convincing evidence that this is so. The hormone is apparently produced by the interstitial cells (cells of Leydig), at least in mammals; in birds and in the lower vertebrates the evidence is much less clear.

The ovary is also an organ producing internal secretions which vary in character and amount at different stages of the œstrous cycle. There is some evidence (obtained chiefly from transplantation experiments) that the interstitial cells are responsible for the maintenance of the normal nutrition of the uterus (which lapses after ovariotomy) and the secondary sexual characters. The follicular epithelial cells (more especially those of the mature follicle) probably secrete a hormone which brings about the phenomena of menstruation and heat. The part played by the corpus luteum is definitely known. It is responsible for the growth and development of the uterus and mammary glands during pregnancy and pseudo-pregnancy (a condition which occurs in monœstrous animals if ovulation is not followed by fertilisation, in the rabbit under certain experimental conditions, and in an abbreviated form in polyœstrous animals). Moreover, there is some evidence that as long as the corpus luteum dominates the ovarian metabolism, the normal ovarian

secretion, which promotes rhythmic uterine contractions, is inhibited; but that when the corpus has reached a certain stage of involution, the ovarian endocrine mechanism, which probably works partly through the intermediation of the pituitary, resumes its activity, and the tolerance of the uterus for the fœtus no longer continues, so that the uterus, responding more readily to internal stimuli from the developed fœtus, contracts strongly, and birth is the result.

CHAPTER VII

HEREDITY AND SEX

It is now generally regarded as certain that the chromatin material of the nucleus, both in the male and in the female generative cells, mediates in the transmission of most, if not all, of the hereditary characters. For although "cytoplasmic inheritance" by means of certain self-perpetuating bodies in the cytoplasm, known as plastids, is supposed by some to take place in special instances, it is not claimed to be a phenomenon of general occurrence, and the evidence relating to it is vague and uncertain.

That the chromosomes, or chromatin filaments of which the nucleus is composed, are of fundamental importance, is shown by a group of well-ascertained facts. With certain exceptions their number is constant for all the body cells in the individuals of the same sex in any particular species, and when it varies it does so in multiples of a definite number, though this condition, which is then called "polyploidy," is uncommon. In the maturation of the germ cells, both ova and spermatozoa, in all species, the number of chromosomes is reduced to one-half (or approximately one-half, since one of the special sex chromosomes may sometimes disappear) of the original number (see above, p. 36).

The fertilised ovum, as already described, contains the full complement of chromosomes. The conclusion that the characters of heredity are localised in the chromosomes was accepted by Weismann, who made it the basis of his famous theory of heredity. This theory assumed (what is now widely believed) that the conjugation of the gametes is the source of variation, and that acquired (as contrasted with innate or congenital) characters cannot be inherited.

The theory of Mendel, first formulated in the middle of the nineteenth century, and rediscovered about twenty-five years

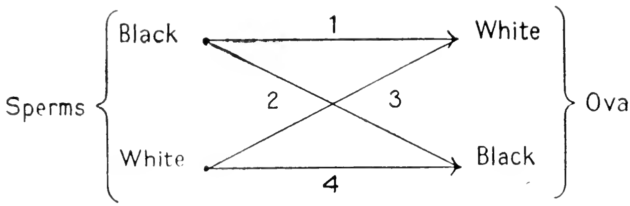
ago, may be said in one respect to be an extension of the theory of Weismann, for it likewise assumes that acquired characters are not transmitted, while its modern developments are susceptible of a confirmatory interpretation derived from the study of chromosome inheritance. It marks a very definite and important advance upon Weismann's theory in that it enables one to discuss variability in terms of the conjugating cells themselves, and not merely in terms of the resulting zygotes.

The original experiments of Mendel were upon hybridisation in peas, the two parent varieties initially selected differing from each other in one particular character. The hybrids produced by crossing were all similar superficially, and resembled one of the parents in the character in question, which was therefore called the *dominant* character, the other character being known as *recessive*. When the hybrids were crossed among themselves, approximately one-half of the offspring were found to be identical with their hybrid parents (dominant hybrids), one-quarter resembled one of the original varieties (the grandparent with the dominant character), while the remaining quarter were like the other pure variety (the grandparent with the recessive character). Consequently the pure dominants and the dominant hybrids resembled one another outwardly, but they differed in their capacity to transmit the characteristics in question, since the pure dominants alone invariably bred true. The recessives also always bred true. Mendel drew the conclusion that in the hybrid the gametes (both male and female) were of two kinds, which were respectively identical with the two kinds represented by the gametes of the original pure varieties. The differentiation of gametes carrying different characters is the essential principle in Mendel's theory, the existence of dominant and recessive characters, though often observable, being by no means universal.

Another example, taken from the work of Bateson and Punnett, will be sufficient to elucidate further the Mendelian conception of gametic differentiation. Breeders of blue Andalusian fowls have always recognised the practical impossibility of obtaining a pure strain of this breed. However carefully the birds are selected they invariably produce two sorts of "wasters," some being pure black, and some white with irregular black marks or splashes. Bateson and Punnett were the first

to supply the explanation. They found that, on breeding from a large number of blue Andalusian fowls, on an average half of the offspring were blue like the parents, a quarter were black, and a quarter were "splashed-white." They consequently drew the conclusion that the mechanism of inheritance in the Andalusian fowl is comparable to what Mendel supposed to exist in his hybrid peas. The gametes of the breed, according to this hypothesis, instead of being all similar and carrying the blue character (as one would suppose on Weismann's theory), are of two different kinds, those of the one kind being bearers of the black character, and those of the other being bearers of the splashed-white character. Such gametes, uniting by chance when the fowls mate together, give rise to three kinds of offspring, one black-white (becoming blue, actually, like the parents), one black-black, and one white-white, these appearing (on an average) in the proportion of 2 : 1 : 1, according to the law of probability. In this particular case of Mendelian inheritance, neither of the two alternative parent characters (*i.e.* neither black nor splashed-white) is dominant and neither is recessive. Why black-bearing gametes uniting with white-bearing gametes should give rise to blue individuals the Mendelian theory does not attempt to explain.

The determiners of the hereditary characters are called factors or *genes*. Thus in the case just described of the Andalusian fowl we speak of the gene for blackness and the gene for whiteness. The cross-bred bird (the first filial or F_1 generation), which is blue in colour, does not carry a factor for blueness but a pair of factors—those for blackness and whiteness—and these are believed to reside independently in the two separate chromosomes of a pair and to become segregated out in the process of gametic maturation, *i.e.* in the reduction division. The birds belonging to the second filial (or F_2 generation) will consist, as already indicated, of one-quarter carrying the factor for whiteness, one-quarter with the factor for blackness, and one-half with both factors in equal numbers as in the F_1 generation. This ratio will be understood by referring to the following diagram in which it is clear that combinations 1 and 4, both of which produce blue offspring, will together compose half the total number:—



Individuals which transmit characters of the same kind, and in respect of this character produce only one kind of gamete, are said to be *homozygous*, whereas those which transmit two (or more) alternative characters, and produce two (or more) gametes corresponding to them, are called *heterozygous*. Thus the blue Andalusian fowl is heterozygous for colour.

In the illustrations just given consideration has been restricted to a single pair of genes, but actually the parental individuals generally differ in respect of a number of character-pairs, and the genes which determine these are inherited independently. Thus, if we cross Aberdeen-Angus and Hereford cattle—two breeds in which the most striking differences are that, whereas the Aberdeen is polled and black and has a face which is not specially marked, the Hereford is horned and red and has a white face—all the individuals in the F_1 generation are polled and black and white faced (these characters being dominant): in the F_2 generation, however, there are no less than twenty-seven possibilities in the way of combinations, though actually only eight appear, as certain of the animals which have different constitutions are superficially alike. It may be stated in general that when two parents which differ in regard to more than one character-pair are crossed, the F_1 generation will exhibit dominant characters irrespective of which parent contributed them.

The fact that so many character-pairs assert themselves independently of one another is supposed to be due to the respective genes being carried in different chromosomes. It follows from this that the number of pairs of characters which can at the same time assort independently in any organism is equal to the number of chromosomes in its cells (Burlingame). Moreover, characters the genes of which are located in the same chromosome are usually linked in heredity. This is the case with the so-called sex-linked characters which are ordinarily transmitted by one

sex only, and are believed to be united within one chromosome with the sex determiner. Examples of such characters are the tortoiseshell colour of female cats, which is transmitted by the yellow male, and various diseases in man. Morgan has shown that sex-linked inheritance is not uncommon in insects as well as in birds. The breaking of such linkage, when it occurs, is believed to take place in synapsis (see p. 37); in this process, which is known as "crossing over," the genes are supposed to pass from one paired chromosome to the other at the time when these are drawn out into slender threads closely twisted about one another so that they are hard to distinguish.

The Inheritance of Acquired Characters

It will be seen that the Mendelian theory, while explaining the inheritance of congenital characters and the mechanism whereby these are distributed among the offspring, takes no account of spontaneous variation. Still less does it in any way suggest a solution of the problem which Darwin set out to solve, viz., the origin of new species. For under Darwin's theory of the formation of new types by natural selection or the survival of the fittest, the fact of variation was taken for granted; this was the material upon which natural selection worked, and no attempt was made to explain how new variations came into existence. It is clear, however, that unless we reject altogether the theory of descent by modification, we must postulate the occurrence at some stage in evolution—and possibly a very remote stage—of the permanent acquirement of new characters, and it is difficult to resist the conclusion that these were brought into being through the action of the environment. This is another way of saying that characters acquired in the life history of the individual through its reaction to its surroundings, must have been transmitted to subsequent generations of offspring.

Of the inheritance of acquired characters in its crude form there is little or no evidence. As is well known, circumcision has been practised by certain races of mankind for a great number of generations, and yet there is no authentic case of a child of such a race being born without a prepuce. So also with dehorning of cattle, which is commonly practised in America; the offspring of such animals are not born polled. The well-known experiments

of Weismann and Cope, who cut off the tails of mice for many generations, were likewise negative, the offspring never being born without tails or with their tails in any way abnormal. A number of experiments by more recent investigators (such as those of Payne who bred fifty generations of flies in total darkness without impairing their reaction to light) have provided no evidence of the transmission of acquired characters.

There are certain other recent experiments in which positive results are claimed, and of these Kammerer's and Pavloff's are among the most notable. Kammerer found that black and yellow salamanders became more black or more yellow, according as they were placed on a black or yellow background, and that their offspring raised on a neutral background showed some of the effects produced on their parents. Kammerer also obtained evidence of the transmission of colour changes in lizards as well as of modifications in the breeding habits of the midwife toad, and the development of horny pads on the digits of the male. The interpretation, however, has been disputed, and Morgan and others regard the evidence as utterly inadequate. Pavloff's experiments were upon mice, but have not yet been described in full. As related they appear to constitute the strongest evidence as yet presented of the inheritance of an acquired character, and they are all the more remarkable in that they relate to a conditioned reflex, a very high form of nervous activity. The mice were trained to run to their feeding place on the ringing of a bell, and the first generation required 300 lessons, that is to say, it was necessary to combine the feeding with the bell ringing for 300 times in order to accustom the mice to run to the feeding place on hearing the bell ring. The second generation, however, needed only 100 lessons, while the third generation required fifty, the fourth ten, and the fifth as few as five lessons. This result is remarkable, but the experiments require confirmation before the conclusions reached can be unequivocally accepted.

In all the experiments so far referred to, the question before the investigator has been as to whether acquired characters or the effects of use or disuse are inherited specifically. In other cases the evidence is indicative rather of the inheritance of a general effect. This is so with Stockard's experiments on the influence of alcohol, and with those of Bagg and Hanson and Little on the effects of radium or x-rays. With many of these

experiments, the malformations, deformities, and signs of deterioration induced, reappeared in the next generation, but speaking generally the organs affected were the most delicate parts or the parts that require the most perfect adjustments in their development, such as the eye (Morgan). Moreover, it is possible that some of the facts are to be accounted for on the supposition that the chromosomes of the germ cells had been directly injured and, consequently, altered in their capacity for hereditary transmission.

Telegony and Saturation

It is still commonly believed by many stock-breeders that a female may be permanently infected through intercourse with a male, so that the latter can impress some of his characters, not only upon his own immediate offspring, but upon subsequent offspring produced by the female as a result of union with another male. Such a phenomenon is called "Telegony" or "Infection." The classic case, and one in which Darwin believed, was that of Lord Morton's Arab mare. This animal was first mated with a quagga and produced striped hybrid offspring, and subsequently on two occasions the mare was mated with an Arab stallion, and both the resulting foals had stripes on the forelegs and back. It was supposed that the striping in these foals somehow resulted from the original mating with the quagga. It has been shown, however, that the presence of stripes is a common phenomenon among several breeds of horses, including Arabs, and that it is specially prone to occur among cross-bred horses, which in this respect may be supposed to have reverted to an ancestral condition. Moreover, numerous experiments, not only with horses (the quagga experiment having been repeated with a Burchell's zebra and various breeds of mares), but also with dogs, fowls, and other animals, have uniformly failed to show any evidence of telegonic influence (Ewart). Again, none of the cases in which telegony has been supposed to occur have stood the test of scientific examination. It may be pointed out, further, that were the telegony hypothesis correct it would involve the inheritance of acquired characters, since the only way in which the characters of a previous sire could be transmitted to subsequent offspring, would seem to be through the body of the mother,

who must be supposed to transmit characteristics which she had acquired either from her former mate or from their joint offspring in the uterus.

"Saturation" is the name given to the supposed process whereby the dam becomes permanently affected by the ova of a particular sire, so that the offspring come to resemble that sire more and more with successive pregnancies. It is merely a description of the cumulative effect of telegonic influence and as a statement of fact is equally devoid of foundation.

The view that a male animal may be infected by a female with which he mates, although not very uncommon among breeders, is even less defensible than the belief in telegony.

Xenia

The term "Xenia," which means "guest-gifts," was applied by Focke to cases of plants in which the male pollen was supposed to affect the ovarian tissue (the seed's substance or the fruit) rather than the embryo itself. The word has also been applied to birds where the colour of the egg laid is said to have been influenced by the cock. Thus canaries, crossed by siskins, linnets, or goldfinches, have been described as having the colour of their egg-shells modified by, and in some sense inherited from, the male which fertilised them. It is, however, extremely dubious as to whether the phenomena of Xenia have any real basis.

Maternal Impressions

The popular belief that mental impressions received by the mother at the time of conception or during pregnancy are transferred to the child as physical peculiarities is devoid of scientific foundation. Nevertheless, it is a very persistent one, and there are innumerable instances of its supposed occurrence, both among man and among animals. Thus an injury or physical impression suddenly produced by contact and accompanied by fright is supposed to result in a birthmark on the child in the position of the injury to the mother; a woman alarmed by an idiot is said to have given birth to a mentally defective child, or a woman chased by a black man to have produced a child who was partly coloured. A common way of giving effect to the belief among breeders of animals has been to paint buildings or fences a

particular colour, where stock are being bred, with a view to obtaining that colour in the young.

Prepotency

It has long been known to stock-breeders that certain sires have the faculty of impressing their characters (or certain of them) upon their offspring, and when these qualities are desirable ones, such a " prepotent " sire is of great value as a stockgetter. Thus a bull may beget female progeny which yield a higher amount of milk than their dams, and so be said to be prepotent for milk production. It has been known also that inbreeding favours prepotency. In the light of Mendelian interpretation prepotency is seen to be a condition belonging to animals which are homozygous for certain dominant factors or genes, and since this condition in general is characteristic of pure bred and inbred animals, it explains why these are so often prepotent over cross-bred or mongrel ones.

The Determination of Sex

We have seen already that the sexual union of the gametes —ova and spermatozoa—is clearly foreshadowed among the Protozoa in the process of conjugation. Bi-parental inheritance is universally correlated with all forms of conjugation, and it may well be that we have here a clue as to the essential meaning of the process. For conjugation, like fertilisation in the higher animals, is productive of variation, since the two gametes are seldom or never absolutely identical.

Variation in the Protozoa was presumably originally due to the direct action of the environment, which must differ slightly even for two individuals living near together, while it is possible, as we have seen, that even among higher forms, apart from the endless variation caused by previous sexual union, the environment, acting through the bodily tissues, may exercise a general influence on the germ cells, if not a specific one.

It may be supposed that the production of further variation induced by conjugation would have a survival value for the organisms concerned, since there would be a greater chance of forms suitable to the environment (which is always changing) being brought into existence. The occurrence of gametic union would

then in itself be directly favoured by natural selection (see p. 6).

We have seen, further, that some of the characteristics possessed and inherited by organisms are dominant in the Mendelian sense, and some recessive, and the perpetuation of useful variations which are also dominant would be favoured by conjugation. Here, again, we have a hint as to the way in which the process of conjugation, once having started, may have tended to continue, for the cell multiplication which follows conjugation was originally no different from the ordinary division which took place when the cell had attained a certain size.

As evolution proceeded certain cells were specially set apart to fulfil the function of conjugation, and these became differentiated into motile cells or spermatozoa, and inert cells, provided with an additional supply of nutriment, or ova. Among some of the Protozoa we find already the beginnings of a gametic differentiation into two kinds of conjugating cells (*e.g.* Vorticella, Volvox).

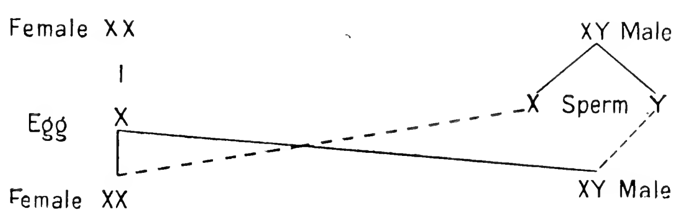
Among the lower animals, as we have seen, the ova and spermatozoa are often produced by the same individual (hermaphroditism), and some forms are alternatively male and female, producing spermatozoa at some times and ova at others, as with the oyster. Amongst the higher animals, hermaphroditism of this sort is not uncommon, and the change from female to male in the progress of individual life is known to occur, even among vertebrates, in isolated cases. It has been suggested that the sexual characters of the male may be present in a latent stage in every female, and the evidence shows that under certain circumstances, a sex reversal may be brought about. Conversely it is possible that female characters are latent in the male, since the change from male to female can also occur (see p. 129).

Nevertheless, among diœcious animals there is usually a clearly defined distinction between individuals which are male and those which are female, and this distinction extends to the chromosome constitution of the body cells. Moreover, it has been shown very clearly, more particularly by Morgan and his school of workers, that there are corresponding differences in the chromosome constitution of the germ cells. It has been found that in most species the gametes of one sex or the other are dimorphic,

that is to say, have two different chromosome constitutions. With most animals, so far as at present known, this difference relates to the spermatozoa, *i.e.* there are two sorts of spermatozoa which differ in the number or kind of chromosomes carried in the nucleus, one sort giving rise to males, and the other sort to females. With some groups, on the other hand, it is the ova which differ (birds, and, among insects, the Lepidoptera or butterflies and moths), and the spermatozoa are all similar. In other words, in most animals the male is heterozygous as regards sex, and the female homozygous, but in some the converse is true.

It has been shown further that in animals of the first kind the sex is correlated with certain special chromosomes called the X-chromosomes, which are somewhat smaller than the ordinary chromosomes or autosomes, and differ from them in their behaviour. Thus the females have two X-chromosomes and the males one X-chromosome, often associated with another chromosome called the Y-chromosome. (The Y-chromosome is still smaller, and may seem to be wanting altogether, so that it was thought formerly that the male had one fewer chromosome than the female.)

When the egg matures one of the X-chromosomes passes out in the reduction division, leaving the egg with one X instead of two. When the spermatozoon matures the X- and Y-chromosomes unite and then separate out, leaving each spermatozoon either with one X or with one Y or, what is more essential, without an X. The fertilisation of any egg (which has one X) by an X-bearing spermatozoon results in a female (XX). The fertilisation of any egg (which has one X) by a Y-bearing spermatozoon (or a sperm without an X) gives rise to a male (XY or simply X). We may express this simply in a diagram :—



Since the two kinds of spermatozoa are produced in equal numbers the males and females resulting from gametic union

will be formed likewise in equal numbers in accordance with Mendelian expectation.

It is noteworthy that the genetic evidence derived from the study of sex-linked characters is confirmatory of the hypothesis just outlined, for it is believed that some characters, like the orange colour of certain male cats or the tortoiseshell colour of female cats, are located in the sex chromosomes. It only very occasionally happens that the linkage is broken, as when tortoiseshell males are produced, and it is noteworthy that these animals, although possessing testes, are sterile.

In the case of birds and Lepidoptera, in which the female is heterozygous for sex, the spermatozoon always has one X-chromosome, while half the ova are without an X-chromosome.

We have seen that the approximate numerical equality of the sexes which is the rule among animals is explained as due to the equal production of male- and female-producing spermatozoa (or ova). The slight divergencies from numerical equality between the sexes which occur from time to time and place to place are caused by subsidiary factors. Since in mammals appreciably more males are conceived than females, it is to be supposed that the balance between male-producing and female-producing spermatozoa is upset at or before fertilisation. The excess of males, however, is considerably reduced during gestation by the high mortality among the males (as shown by Parkes). This equality mechanism, which we must regard as primitive, having become established, is maintained even among polygamous animals where it has ceased to be useful, since one male is the physiological equivalent of a large number of females, a fact which is taken advantage of by man, who castrates by far the larger number of males among domestic animals for economic reasons, keeping only the best for stud purposes. This superfluity of males may, however, have favoured the conditions under which preferential mating has been supposed to operate, as postulated by Darwin's well-known theory of Sexual Selection. This theory was propounded to supplement the theory of Natural Selection or the survival of the fittest, and to account especially for those secondary sexual characters, usually of the nature of embellishments, such as the wonderful colouring of many birds and insects, the bird's power of song, the tail of the peacock and pheasant, and that of the bird of paradise, as well as the antlers of the

stag, the horns of the stag-horn beetle, and many other such structures or peculiarities. It was supposed that the female exercised an æsthetic capacity in selecting her mate, thus favouring the hereditary transmission by the male of those qualities of form and beauty which pleased her fancy best. Moreover, the combats between rival males for the possession of the female, such as occur during the rutting season of the stag, would result in the more vigorous males, and those with the best weapons of offence, coming off victors, and so surviving to perpetuate these characters in their young.

Sex Reversal and Intersexuality.—Notwithstanding the fact that the two sexes are ordinarily correlated with the chromosome constitution it is apparent that under certain circumstances the latter may be overridden, and an animal may possess some or all of the characteristics of one sex in conjunction with the chromosome constitution usually associated with the other. Thus an animal may be a male and produce spermatozoa which are fully capable of fertilising ova, and yet have two X-chromosomes in the cells of the body. Moreover, as already stated, there is evidence that all animals have in some degree the potentialities of both sexes, and even among the higher vertebrates true hermaphrodites are not unknown. It is evident, therefore, that apart from the chromosome constitution there must be some other mechanism upon which the sex of the individual depends.

True hermaphroditism (*i.e.* the existence of testicular and ovarian tissue within the same individual) in man is exceedingly rare, but a few cases have been described (see Lipschütz), and of these Blair Bell's and Berblingler's are of special interest. In each there was a marked change of sexual characters from female to male, and an ovario-testis was found with Graafian follicles and seminiferous tubules containing cells that were probably spermatogonia, but no actual spermatozoa.[1] Menstruation took place before the reversal set in, and recurred normally for a few years, after which it stopped. In these and other instances (in many of which so far as recorded the hermaphroditism did not extend to the gonads) there were changes in the external characters as well as in the psychology. Thus in Blair Bell's case, hair grew on the face and other parts of the body, and the clitoris

[1] These individuals, therefore, differed from functional hermaphrodites such as we find occurring normally in many invertebrates.

enlarged and became enveloped in a prepuce. Apart altogether from the essential generative organs there are all degrees of somatic and psychical intersexuality in man, as instanced by the sapphist and the virago, on the one hand, and the effeminate man on the other. Moreover, some authorities regard homosexuality as an intersexual condition.

Among the lower mammals intersexuality has been especially noted in pigs and goats. Pick examined half a million pigs in the Berlin slaughterhouse and found six cases of true glandular hermaphroditism. Krediet has described a goat with a definite ovario-testis. Numerous cases of intersexuality in horses, cattle, sheep, goats, and pigs have been described by Crew. The genital organs generally consisted of a testicular gland with tubules and interstitial tissue (but without spermatozoa), vasa deferentia, vesiculæ, a prostate, an enlarged clitoris, a uterus, and a vagina. Many of them were probably cases in which sex reversal had taken place, the ovarian tissue having atrophied. Hammond has presented evidence of reversal in rabbits, the ovaries containing structures suggestive of incipient seminiferous tubules. In some individuals (human and other) the masculinisation of a female was associated with an abnormal growth (hypernephroma or neoplasm) in the suprarenal glands.

Among birds sex reversal appears to be commoner. A number of instances of sex change have been recently described (Pearl and Boring, Crew, Hartman and Hamilton, etc.). Miss Fell has given an account of the microscopical structure of hen's ovaries, showing sperm formation after sex reversal had set in. In one of these the hen had formerly laid many eggs, which duly hatched into chicks, but she afterwards changed into a functional cock, and became the father of two chickens. The so-called "cock-feathering" of old birds has long been known, and Gurney has described its occurrence in twenty-six species. Darwin also alluded to the crowing of old hens and other similar phenomena.

Sex reversal may relate also to the mating habits of birds under natural conditions, for in the crested grebe Julian Huxley has described the male as sometimes adopting the position of the female and vice versa, and the same thing has been seen exceptionally with pigeons.

Various degrees of hermaphroditism in Amphibia have long been known, and hermaphrodite frogs have often been described.

Champy has recorded the gradual transformation of the external sex characters of the male newt (*Triton cristata*) into female ones as a result of abnormal nutritive conditions. The gonads also changed. Crew has described a most interesting instance of sex reversal in a frog which changed from a fully functional female to a fully functional male. In the latter condition the frog copulated with females and had 774 offspring, and it is especially noteworthy that every one of these was a female. This is believed to have been due to the frog, which started as a female, having a female chromosome constitution. Julian Huxley, in referring to certain very unusual sex ratios in the young of the millions fish (*Girardinus pœciloides*), is disposed to explain these as due to sex reversal on the part of one of the parents in the same kind of way as occurred with the frog observed by Crew.

Intersexuality is very common among insects and other arthropods. It has been recorded by Sexton and Julian Huxley in *Gammarus*, by Keilin and Nuttall in lice, and notably by Goldschmidt in the gypsy moth. As further proof of the existence in the same individual of the potentialities of both sexes, the phenomena of "parasitic castration" may be cited. Giard was the first to observe that in certain male crabs (*e.g. Stenorhynchus*) affected by other Crustacea parasitic upon them, not only were the gonads destroyed, but the host assumed some of the characteristics of the female. It was afterwards found by Smith and Potts that in allied genera (*Inachus, Peltogaster*) the "parasitised" male crabs developed egg-bearing appendages on the abdomen like those of the normal female and afterwards produced eggs. The testis, therefore, changed into an ovary. "Parasitic castration," therefore, is really sex reversal. It is remarkable, however, that in this case the metabolism changed first, fat and lutein being formed as in the female, while the glycogenic function, which is more characteristic of the male, was depressed. Smith concluded that the parasite acted upon the male host as the ovary does in the female and called forth fat production, whereby the normal female individual is able to withstand the drain on the system incurred by egg formation, and this condition having been brought into existence, stimulated the sexually indifferent germ cells to develop after the manner of the female. Courrier has lately shown that when the male of the common shore crab

(*Carcinus mænas*) is infected with the cirrhipede, *Sacculina*, certain of the female characteristics may develop without the testes being destroyed.

Experimental Sex Reversal and Intersexuality.—That the chromosome constitution of the sexes may be overridden is shown further by those experiments in which ovaries have been transplanted into males and testes into females, the animals employed having been previously deprived of their own gonads. It has been shown above that in the higher animals, at any rate, the secondary sexual characters are dependent upon the influence of stimulating substances secreted by the sex glands. The experiments of Steinach, Lipschütz, Athias, Sand, Moore, and others have demonstrated further that an intersexual condition or almost complete sex reversal may be brought about by ovarian or testicular transplantation after previous castration. Thus if ovaries are grafted into castrated male rats or guinea-pigs, not only will the mammary glands develop and secrete milk, but the sexual reflexes and psychic behaviour may likewise change. Guinea-pigs so operated upon may display the "tail-erect" reflex of copulation, and the "kick-guarding" reflex, which is used by the female to ward off the male when the former is not in a condition of œstrus. Conversely, in spayed females with transplanted testes, the clitoris becomes transformed into a penis-like organ, and even the horny styles, which are characteristic of that organ in the male guinea-pig, undergo a marked development. Experiments which illustrate the same point have been performed upon birds by Goodale, Pézard, and Zawadowsky. Thus Pézard transplanted an ovary into a castrated cock and found that it caused the suppression of such male characters as the spurs.

Experimental hermaphroditism has also been successfully performed, as in Sand's experiments upon rats, when the ovaries were grafted within the tissue of the testes. The results of experimental hermaphroditism have been various, some animals displaying to a large extent the characters and psychic behaviour of both sexes (*e.g.* development of mammæ and normal penis with reversible sexual behaviour). According to Lipschütz the results probably depend upon variation in the quantitative production of the male and female hormones at different times, these tending to act antagonistically.

The Free-Martin.—When cows have twins it sometimes happens that one calf is a normal fertile bull and the other a sterile individual, which is generally regarded as an abnormal female with some of the characters of a bull. This is called a free-martin. There is considerable variation among free-martins, but in the more typical examples an enlarged clitoris is present, and internally vesiculæ seminales and vasa deferentia are generally represented, though in an undeveloped state, together with a rudimentary uterus. The gonads are often testis-like, but they contain no spermatogenetic tissue, and are retained in the body cavity; sometimes they appear to be undeveloped ovaries.

It was at one time suggested that the free-martin, together with its co-twin, might arise from a single ovum. That two embryos may originate from the segmentation of one ovum is known occasionally to occur, but in such cases the two individuals usually bear a very close likeness to one another, so much so that they have been compared with looking-glass images, and they are described as "identical twins." The fact that the free-martin and its partner are not derived from the same egg is, however, definitely negatived by there being two corpora lutea in the ovaries of the mother, thus showing that two follicles had ruptured and two ova had been discharged.

The probable explanation of the free-martin was discovered by Lillie in America, and independently by Keller and Tandler in Austria. They found that the chorionic membranes of the two embryos—the free-martin and its twin male—were fused together, and not only this but the blood vessels were also connected together so that there was a common circulation between them. This suggested that substances formed in one of the embryos would pass to the other and modify its development. In view of the other known facts about hormonic action in modifying sex it was natural to suppose that the free-martin started its life as a female, but was acted on by the male hormone coming from the bull twin. Moreover, it was shown that when two embryos are present without any connection between the chorionic blood vessels they both develop normally and there is no free-martin produced. Furthermore, it was shown that the testis in the male calf develops more rapidly than the ovary in the female, and so may be supposed to exercise its influence

over the sexual characters at a time when the ovary is still rudimentary; and lastly, Lillie and Bascom have been able to demonstrate an embryonic interstitial gland in the testis of the bull calf, and it is to this gland that the masculinising influence is ascribed. The free-martin then is an intersexual individual, its condition being determined by a hormone arising from the embryonic testis of its male twin. Keller has demonstrated a similar intersexuality in the goat and shown it to be due to chorionic union in the same way as in the cow.

Minoura states that he has produced intersexuality experimentally in the chick by removing a portion of the egg-shell during the second week of incubation, and grafting on to the vascular area of the chorio-allantoic membrane a portion of a gonad of another bird belonging to the opposite sex. The grafts were taken from birds of all ages, from ten-day chicks to mature birds. During the remainder of the incubation period, after the operation (from six to twelve days), intersexual individuals of all grades were formed. These intersexual chicks are regarded as artificial free-martins, the stimulus for the abnormal sexual development being derived from the transplanted gonad. This explanation has, however, been questioned, and the suggestion made that the abnormalities produced were the result of interference in normal development (Greenwood).

In view of these experiments and the observations made upon the condition of life of the free-martin, the question arises, why in mammals intersexual individuals are not habitually produced from those which start as males owing to the influence of sexual hormones arising from the ovary of the mother? No definite answer can be given to this question, but it is suggested that the hormone may be in some way arrested from penetrating through the placenta, which, as we have already seen, appears to exercise a selective action over some of the substances which transfuse to the fœtus, the maternal and the fœtal circulatory systems being always quite distinct, without any union of vessels, such as is found between the chorions of the free-martin and its twin.

Goldschmidt's Theory of Sex-Determination.—We have seen that the sex of the future individual, in many animals at least, is apparently determined by the chromosome constitution of one or other of the gametes which unite to form the zygote producing

the embryo. We have seen also, what at first sight seems contrary to this conclusion, that the sexual condition may depend upon hormones arising in the gonad, and that under certain circumstances, both natural and experimental, the chromosome constitution may be overridden through the action of such hormones, and the determined sex be reversed or intersexual individuals produced. These two groups of facts are reconciled under Goldschmidt's hypothesis of sex-determination.

According to Goldschmidt the X-chromosome carries the gene of an enzyme-producing [1] character, the enzyme being a female-determining one in cases where the male is heterozygous for sex, while the Y-chromosome, or more probably the cytoplasm, carries the gene of a male-determining enzyme. If there are two X's in the zygote, the female enzyme being present in double quantity causes the future individual to be a female. If there is only one X, the female-producing enzyme is overpowered by the cytoplasmic enzyme, and a male results. The enzymes are not destroyed, they are only overpowered. Now by the chemical law of mass action, the rate of the reaction is proportional to the active mass of the reacting substances. These in the case under consideration are represented by the sex enzymes and the somatic substances. The sex enzyme in excess, therefore, will have a start over the other enzyme. When, however, a certain amount of the first enzyme has been used up, the rate of its reaction will fall; the fall will occur first with this reaction since it will have taken place quickest. Then the slower enzyme will, so to speak, overtake it, and at this point a change of sex will begin.

With insects this does not usually happen at all, for the insect is a short-lived organism and dies first. In many other animals, such as birds and mammals, the sex change is inhibited by the ovary, but if the ovary is destroyed by a tumour, as sometimes happens with fowls (Crew), a change of sex results. Moreover, there are normally signs of sexual change in older birds, and even in mammals after the menopause (though these are regarded by some rather as a reversion to an indifferent or neutral condition). The results of parasitic castration are susceptible of a similar interpretation.

[1] The idea that the substance in question is actually an enzyme is a purely speculative one.

In insects the gonads exercise no influence over the secondary sexual characters, or even over the sexual instincts. This is explained by Goldschmidt on the assumption that the production of the sex hormones in these animals is not localised in special organs, but takes place within all the cells of the body. It is impossible, therefore, to obtain "Hormonic Intersexuality" in insects, but "Zygotic Intersexuality" can be obtained as Goldschmidt has demonstrated in an extensive and elaborate investigation with cross-breeding the gypsy moth (*Lymantria dispar*). In crossing a male of a European variety with a Japanese female the first generation of crosses (or F_1's) are either males or intersexual females. In the converse cross, all the F_1's are normal males or normal females, but the F_2's are intersexes. Goldschmidt has elaborated the idea of "strong" and "weak" races. Thus a "strong" male mated with a "weak" female will produce female offspring, but these will show modification towards the male condition, while the males will be normal. Goldschmidt explains these results on the ground that though the female-producing factor is normally stronger than one X, a male factor from a "strong" race has a quicker action than normal, and in time overpowers the female factor with the result that a moth which has started as a female afterwards develops certain male characters. Two X's, whether from "strong" or "weak" races, produce the usual result, *i.e.* a normal male (see p. 136, footnote). There are various degrees of strength in the different races of gypsy moth, and the sexual characteristics of the offspring depend upon what crosses are made. In this way, a complete scale of intersexuality may be obtained.

Birds are supposed in some degree to resemble insects in that all the cells may contain both sexual formative substances. In this way Goldschmidt interprets "gynandromorphism," which occurs in both insects and birds. It is a condition in which one side of the body has male characteristics and the other female, the actual gonads also being often different so that the animals are hermaphrodite. Poll's bullfinch and Weber's chaffinch are well-known examples of bilateral gynandromorphism. Anterio-posterior gynandromorphs have also been described, as in the case of Bond's pheasant.

Gynandromorphism cannot occur in mammals which represent the last stage in the centralisation of the control of sex differentia-

tion, this having been completely (or almost completely) transferred from the individual cells of the body to the hormone-secreting cells of the gonads. Thus sex reversal can be most readily induced in mammals, because hormone production is localised in organs which can be removed and transplanted. The zygotic constitution originally called these organs into being, but their independence having been once established, their modes of action can be investigated irrespectively of the zygotic constitution.

To the question what it is that the sex enzymes—which themselves depend upon the chromosome constitution—produce as the end products of their activity, Goldschmidt answers, "the hormones which are responsible for the modelling of definitive sexual form."

A further point on which both Goldschmidt and Lipschütz lay considerable stress is that the variability of intersexual types is due to the differences in the quantitative relations between the male and female hormones, these varying with the passage of time. Thus sex-inversion will take place the earlier the greater the amount of the heterosexual hormone (the second one to act) above the normal, and the extent of the change is the more pronounced the sooner the heterosexual transformation begins in the development of the individual. Moreover, those organs which are differentiated very early in embryonic development do not usually undergo heterosexual change, and in the gypsy moth the gonads are the last organs to be affected.

To the further question as to what factors are capable of producing a quantitative disturbance of the hormonic activity of the sex glands, no complete or satisfactory answer can yet be given. It is known that tumours of the suprarenal bodies may be the cause, and also that abnormal conditions in regard to food and environment may apparently have the same result, as with Champy's newts, while "parasitic castration" in crustaceans and insects seems to supply other instances. But it is impossible to formulate any general principle applicable to all the known phenomena. There is, however, an accumulation of evidence that the gonads (and even the peritoneal epithelium) may contain neutral germinative elements which can develop along the lines of either sex, if the appropriate stimuli are present (Gatenby). It must, however, be emphasised that intersexuality

on any considerable scale and affecting many individuals is the exception and not the rule, and it would be unreasonable in the present state of our knowledge to expect a theory of sex-determination to account fully for every known case.[1]

Other Theories of Sex-Determination.—Innumerable theories of sex-determination have been put forward in the past, but none of these has been satisfactory or applicable to more than a limited number of facts. According to one theory the right ovary produces ova of one sex and the left of the other (Dawson), but this view is negatived at once for birds, which have only one ovary, and for those animals in which one ovary has been removed. Another theory affirms that the sex of the future offspring depends upon the time of copulation during œstrus, and this again has been disproved for special cases. The effects of feeding have often been made the basis for theories of sex-determination, and while it is possible that they may account in part for exceptional cases of sex change, no hypothesis so far put forward has been found to be of general application. On the other hand, it is evident, in the light of many of the ascertained facts referred to above, that the other theories of sex-determination must be rejected, though certain of them have not been without value, since they have stimulated inquiry, and led to an accumulation of evidence bearing on more than one problem of biology.

[1] In connection with Goldschmidt's theory of intersexuality in the gypsy moth, it must be remembered that in the Lepidoptera the male is homozygous for sex and the female is heterozygous (see p. 126). Consequently the male has two X-chromosomes in the body cells and the female one X, or the exact reverse of what occurs in most other animals as far as is known.

CHAPTER VIII

FERTILITY

We have seen that among the individuals of the higher animals whereas the number of ripe ova released is small—in many species usually only one being discharged at any single œstrus—the number of spermatozoa produced by the male and ejaculated at insemination is extremely large. It follows that in a certain sense the female is a more important factor in fecundity than the male—that is to say, that the number of young in a litter is mainly controlled, if not determined, by the mother rather than by the father. There is another sense, however, in which the male may be said to be the more important factor in fecundity. With the domestic animals it is customary for one male to mate with a large number of females: thus in ordinary practice, a stallion will serve some eighty mares in a season, a bull will mate with 80 to 120 cows, and a ram will cover fifty ewes. If for any reason the stud animal is lacking, or partially lacking, in reproductive capacity, so that some or all of the females served are sterile, the practical results are far more serious than if any one individual female is wanting in fertility. Moreover, it sometimes happens with human beings that the woman is held accountable for failure to have children when in reality it is the male partner who is at fault. Such sterility may be caused by disease, or it may be due to some abnormal condition, such as excessive poverty of nutrition or adiposity, the latter being a commoner cause.

Effects of Environment and Nutrition

That the generative system is peculiarly susceptible to changed conditions of existence has been recognised from early days. Thus Aristotle commented on the increased fertility of sheep in a favourable environment. It is well known that the domestic animals not only breed oftener, but also produce larger

litters than wild animals belonging to the same species. On the other hand, certain wild animals, when removed from their natural conditions and brought into captivity, become partially or completely sterile; the Indian elephant, for example, seldom breeds under domestication, although kept in a perfectly healthy condition and in its native country. It would seem that in the absence of the normal stimuli the generative system somehow fails to discharge its functions, and this failure may take the form either of absence of sexual desire (impotence) or of incapacity to produce active spermatozoa or ripe ova.

In animals which, as a general rule, breed freely in a state of confinement or domestication, there is no doubt that nutrition plays a very leading part in regulating the capacity to produce offspring. Very fat animals not only have fewer young, but come on heat less frequently. In the male spermatogenesis is partially inhibited. In the female there is a greater amount of follicular atrophy, the ovarian metabolism being disturbed by the deposition of fat. Follicular atrophy is likewise common in under-fed animals, and may take place as a result of suckling. It is known also that menstruation in women, as well as the capacity to produce ripe ova, are liable to be inhibited by lactation, but this is by no means invariable.

The practice of "flushing" sheep, that is, supplying them with cake or corn or turnips, or putting them on superior pasture, for a few weeks before and during the sexual season, is well known to result in a larger crop of offspring at lambing time. This is because it induces a larger number of follicles to ripen and of ova to be discharged at the œstrous periods. Once the ewes have become pregnant, the "flushing" may be discontinued, since the number of embryos has been already determined at ovulation. It is recognised also that a good thriving or improving condition at the sexual season in any farm animal is the one most satisfactory for getting the maximal number of young.

Fœtal Atrophy

In some domestic animals, however, and more particularly in the sow and tame rabbit, which produce large litters and not one or two (or less commonly three), as in the sheep, fecundity may be conditioned rather by the factors controlling development

in utero than by the production of ova. In such animals the number of eggs matured is frequently in excess of the nutrition available for them, and this leads to atrophy as newly fertilised ova or partially developed embryos (Hammond). Fœtal atrophy has also been described in certain wild animals (rat, mouse, etc.), but is uncommon.

Hammond has shown that fœtal atrophy cannot be due to bacterial infection since the uterus is aseptic. Neither is it due to overcrowding in the uterus, since this organ is capable of great expansion; moreover, the distribution of the degenerate fœtuses is irregular and does not suggest that death is due to overcrowding. Hammond supposes that the phenomenon may be due to adiposity, or to inbreeding, or to a genetic "lethal factor" (that is, something inherent in the embryo itself), in the same kind of way as Kirkham found with the homozygous yellow mice which are never brought forth alive, but die *in utero* during implantation.[1]

Vitamines and Fertility

It is now known that sterility may be due to the absence of vitamines or accessory nutritive substances, the presence of which is essential for normal metabolism, undergrowth or "deficiency diseases," such as scurvy or beri-beri, occurring when one or other of the vitamines is absent. Evans and Bishop claim further there is a vitamine present in green food which has a specific connection with the generative processes, and that in the absence of this vitamine fœtal absorption occurs. Further, Parkes and Drummond have shown with rats that in the absence of the "water-soluble vitamine B" (the deficiency of which is associated with "beri-beri"), neither sex is able to produce gametes, so that the animals are completely sterile. It is possible that some of the cases where captivity or a change of environment appear to cause sterility may be accounted for by the absence of the necessary accessory food substances from the diet.

[1] Hybrid yellow mice of a certain type when interbred should produce, according to Mendelian expectation, one pure non-yellow (*e.g.* black), two hybrid yellow, and one pure yellow. Actually only two yellows are produced for one non-yellow, the pure or homozygous yellows dying before birth. Lethal genes have also been found in the vinegar fly, *Drosophila*, as well as in a breed of cattle.

Reduced Fertility as a Result of Inbreeding

The fact that inbreeding may result in a reduced fertility or even in complete sterility has already been discussed in dealing with the fertilisation of the ovum. It was pointed out that as a practical matter inbreeding often results in an apparent loss of vigour, this being manifested in a variety of ways, one of which is an increasing tendency towards sterility. At the same time there is a growing body of evidence to show that different degrees of productivity, down to complete sterility, may be inherited as though they were Mendelian units or genes. In the light of this conception the effects both of inbreeding and cross-breeding would seem to acquire a new significance. It has been shown that in some insects (*Drosophila*) complete sterility may be a sex-linked character. In certain inbred strains of cattle and other domestic animals it has been suggested that a factor for sterility was present. Thus in the famous Duchess family of Shorthorn cattle, which eventually became extinct, it is possible that a sterility gene formed part of the factor complex, and that this, as a result of close and continuous inbreeding, kept on reappearing with increased frequency until no more fertile animals were produced. Moreover, it has been shown that with *Drosophila*, as also with the rat and the guinea-pig, a high degree of fertility can be maintained in successive generations of inbred animals by selecting from the more fertile individuals. Further, there is direct cytological evidence that in *Drosophila* sterility may be correlated with the absence of a particular chromosome (Morgan).

Conversely, the increased vigour and fertility brought about by cross-breeding may be due to the establishment of a more excellent factor-complex rather than to any mysterious stimulation effect of the heterozygous condition.

An example taken from the work of Emerson upon maize breeding, in which the same principles hold, will make this clear. A dwarf race of maize which was almost completely sterile was crossed with a tall plant so deficient in chlorophyll production that it was unable to produce seed, although it had some functional pollen. The cross-bred plants, on the other hand, were tall, dark green, and produced well-developed ears. Here, normal stature was contributed by one parent and proper chlorophyll

development by the other. The progeny thrived and became highly productive. The success of this result is believed to have been due to the complementary action of two dominant factors rather than an unintelligible stimulation effect brought about by the cross. The general evidence as to the effect of inbreeding is that it promotes homozygosity of genes, and this produces uniformity of characters. Unfortunately for the practical breeder, the homozygosity is very often for genes of harmful or undesirable characters, and that is why the process must be accompanied by careful selection. On this view, if the undesirable genes can be eliminated and only useful ones are allowed to remain so as to be perpetuated, the final result should be all to the good. It is suggested that it was the practical adoption of this principle by certain of our famous breeders, such as Bakewell and Cruikshank, which led to some of the most highly successful results that have been attained in the breeding of domestic animals.

Cross Sterility between Species

The sterility of hybrids between species is a very common, not to say usual, phenomenon, but its cause is still largely an open question. Such infertility, however, is by no means invariable. Thus, species of the dog genus (*Canis*) will breed together exceptionally and produce fertile offspring. The various members of the family of Bovidæ or cattle are known to do the same, even though the parents belong to what are ordinarily regarded as different genera (*e.g.* the cow, *Bos taurus*, and the bison, *Bison americanus*).

In some hybrid animals the generative organs are imperfectly developed, and in most the gametes are not formed. It has been suggested that the sterility is due to irregularities in the mechanics of division in the germ cells, and in some hybrids the number of the chromosomes derived from each parent is different, but this is not invariable.

Blakeslee has shown that in the plant *Datura* a new variety or mutation may arise with double the number of chromosomes (Polyploidy, see p. 115), and that this form is sterile with its parent. This discovery is of great interest in relation to the problem of the origin of new species—the central problem which

Darwin set out to unravel, but which in spite of long-continued experimental investigation has so far resisted solution.

Multiple Births

The number of offspring born at a time, that is, the number of young in a litter, is approximately constant for each sort of animal, but there are often differences in this respect between varieties and even between families. In man, single births are the rule, twins occur in rather more than 1 per cent. of births, and triplets once in six or seven thousand (the estimates varying rather widely). Quadruplets and quintuplets are very rare, especially the latter. Among animals, the mare and the cow usually produce only one young at a time, but occasionally two, and the sheep either one or two (sometimes three, but very rarely more). The sow and bitch, on the other hand, may have much larger litters, the sow sometimes producing as many as seventeen or even twenty piglings.

It occasionally happens in multiple pregnancy that the offspring are by two different sires. Thus it has been known that a woman has had intercourse with two different men within a short time of one another, one white and one coloured, and nine months afterwards has given birth to twins of different colours. Among dogs, mixed litters got by more than one sire are not very uncommon. Such a phenomenon is known as *Superfecundation*. It more rarely happens that as a consequence of ovulation and coition during pregnancy—both of which are abnormal—the uterus may contain embryos of two different ages and sizes, but no authentic case of this has been recorded for man. This condition is called *Superfœtation*.

Inheritance of Fertility

Like other racial characteristics, fertility is inherited. This has been proved for horses, sheep, and pigs, as well as for poultry, and it has also been established that an increased fertility can be transmitted through the male to the next generation of females, in just the same kind of way as the deep milking properties of cattle are transmitted through the bull to the next generation of cows. In certain breeds of fowls Pearl has found further that one of the factors for increased egg-production is sex-linked,

being present in the cock only, and transmitted by him to the next generation of hens. With man, Pearson has found that fertility is inherited equally through the male and female lines.

Artificial Insemination

An account of all the anatomical and other conditions which cause sterility is outside the scope of this book. Attention may, however, be drawn to those individual peculiarities which may be overcome by resorting to artificial insemination—that is, the injection of semen into the female passages at the season of œstrus or about the time when ovulation is believed to occur.

Artificial insemination in a mammal was probably first demonstrated in the eighteenth century by the Italian naturalist, the Abbé Spallanzani, though there is evidence that it was not unknown to the Arabs in very much earlier times (Heape). Spallanzani succeeded in impregnating a bitch spaniel in this way by injecting semen, obtained from a dog by spontaneous emission, into the vagina of the bitch, which in due time gave birth to a litter of pups. Since Spallanzani's time artificial insemination has been practised successfully upon mares, cows, and other animals, and usually with a view to curing sterility. It has also been performed when it was desired to get crosses between animals showing great disparity in size (making normal coition difficult), as in Millais' experiments in which bloodhounds were inseminated with spermatozoa obtained from Basset hounds (a much smaller breed). Moreover, Ivanoff has recorded an experiment in which he inseminated a mouse with the sperm of a rat and obtained two hybrid young ones.

Artificial insemination as a means of overcoming certain forms of sterility in women has been performed by various medical men from the time of Hunter in the eighteenth century. The method adopted is to inject the semen directly into the uterus through the os, by means of a syringe, the fluid in most cases being obtained from the vagina of the same individual. In this way it has been found possible to overcome such structural defects as constriction or undue rigidity of the os uteri, or hypertrophy of the lips of the external os. By modifying the method by which the semen is obtained it has proved possible to induce pregnancy

in cases of abnormal vaginal secretion, where the spermatozoa are apt to be killed before they can effect an entrance into the uterus, and in other cases where there is an inability on the part of the vagina to retain the semen after coitus.

Artificial insemination has been practised on mares with highly successful results, many valuable animals having been in this way saved for breeding, when otherwise they would have been sterile. Moreover, several individuals may be successfully impregnated as a result of one service by a male.

Other Causes of Sterility

Sterility may be due to diseases of manifold kinds, both those affecting the organism as a whole, and those relating to the generative organs (such as the venereal diseases), but the consideration of these belongs to the science of pathology and is outside of the subject of this book. Failure to produce offspring may also be due to sexual aberrations, resulting in impotence or absence of normal desire. Such conditions are not necessarily harmful in themselves and may be consistent with normal health and well being. Some of them are to be regarded as psychological manifestations of a congenital intersexual state comparable to those intermediate sexual conditions which occur in many animals. They probably have a hormonic basis.

Sexual aberrations are usually deviations from the normal processes, and most of them have been observed in some degree in the lower mammals under conditions where it is impossible to gratify the usual impulse. This is the case with masturbation, the evil consequences of which were formerly much exaggerated. There can be no doubt, however, that masturbation, when carried on to excess, is exceedingly harmful and may lead to impotence, but it is also true that over-indulgence of the normal sexual impulse is deleterious. With animals in a state of nature, the possibility of sexual excess is guarded against by the prolonged periods of quiescence, but as is well known to stock breeders, too frequent sexual intercourse or indulgence at too early an age has a deteriorating effect upon the male kept for the purpose of the stud.

Abortion

The frequency of occurrence of abortion shows a considerable range of variation, but it is often an important factor in determining a low fertility. With women the frequency of abortion (including premature birth) as compared with birth at full term varies according to different authorities from one in five to one in ten. (The term abortion or miscarriage is usually applied to cases occurring up to the beginning of the seventh month; to cases after that time, when the child has become viable, the expression "premature labour" is usually applied.)

Abortion in women is usually heralded by an excessive hæmorrhage which is sometimes mistaken for menstruation. If, however, the embryo comes away, the bleeding usually ceases within a short time. Not uncommonly, however, some of the embryonic tissues are retained and hæmorrhage continues and may become dangerous. Abortions should never be disregarded as incidents of no importance, and professional assistance should always be obtained.

Abortion occurs also in all the domestic animals and occasions considerable annual loss to breeders. It may assume epidemic proportions, when it is due to a particular bacillus which is usually different for each species. Contagious abortion among cattle is especially common and is brought about by a bacillus affecting the placenta (Bang).

Apart from contagious abortion, the causes of the phenomenon are very various, and may be psychological, physiological, or pathological. Deliberate abortion (as by certain drugs such as ergot or by mechanical means) in women is a punishable offence, but nevertheless is sometimes carried out. Involuntary abortion may result from any kind of strain or from fright, both of which are common causes with the domestic animals and sometimes also with women. In the mare abortion is especially apt to occur between the sixth and ninth weeks of pregnancy, since about this time the embryo loses its primitive attachment through the yolk sac before acquiring its more permanent connection by means of the chorion. The process of "slipping foal" at this time may be regarded as a reversionary one, since, in the marsupial, the yolk sac is (in most species) the sole organ of fœtal nourishment, and release from it marks the act of birth.

The occurrence of fœtal atrophy and its possible causes have already been discussed.

Rate of Propagation

Among amphibians, fishes, and a very large number of invertebrates, probably the majority of the ovarian eggs are actually spawned, and here the rate of propagation is regulated by the number of eggs which become fertilised and, escaping the many dangers to which they are exposed, are able to complete the process of development. Thus it is stated that the cod spawns six million eggs, less than a third of which become fertilised. In the higher animals, however, as well as many of the lower, only a certain proportion of the potential eggs formed in the ovary ever reach maturity at all, and a still smaller percentage are released from the organ so as to obtain a chance of becoming fertilised. Balfour was the first to show that in the rabbit one embryonic egg may develop at the expense of others, and that the eggs which disappear may serve as food material for the one ovum which, owing to a superior vigour or to some chance circumstance relating to its position in the ovary, was able to survive. Thus, there is a veritable struggle for existence amongst the gametes during the process of development within the gonads, and those gametes which survive may do so by taking advantage of the death of others at a very early stage of existence. Arai has estimated that the ovary of the rat at birth contains 35,100 ova, but that these are reduced by degeneration to 11,000 after twenty-three days, and to 6,000 by the sixty-third day. We have seen already that nutrition plays an important part in regulating the proportion of the eggs which survive, so as eventually to become mature.

The Birth-Rate in Man

Statistics show that the birth-rate (that is, the proportion of children born annually to the total number of the population) in civilised countries has for some years past been declining. This is true not only of the countries of Europe but in most parts of the Western hemisphere where European races have settled, as well as in Australia and New Zealand. In France the actual population has been approximately the same for the last three

decades, but in some years there has been an excess of deaths over births, and this not only during the war. France, however, is exceptional, for in other civilised countries, although the birth-rate is decreasing, the population is still increasing; and it is already evident to those who have studied the question that, unless something unconceived of occurs, this increase cannot be continued much longer without a general lowering of the standard of life, which will lead gradually to a struggle for existence growing ever more intense, and reacting in the worst manner possible upon every phase of human activity. Indeed, some of the attendant evils of over-multiplication are already making themselves felt; we have only to cite the unemployment problem, the difficulties due to overcrowding and the shortage of houses, the encroachment of the towns upon the country, and the consequent defacement of the countryside.

Statistics show further that the birth-rate varies widely among the different social classes. Speaking generally, the wealthiest people have the fewest children, and as the income decreases the size of the families increases, the unskilled workmen having the largest number of children. Furthermore, the greatest rates of reproduction are too often shown by the less fit elements in society, and it is noteworthy that the birth-rate of the feeble-minded is 50 per cent. higher than that of normal persons, and that feeble-mindedness is an hereditary defect. It is the object of the science of *Eugenics*, founded by Francis Galton, to combat this evil, and to ensure, as far as possible, that future generations should be recruited from those members of the community who are the healthiest and most vigorous, both mentally and physically. So far, however, as the population question is one affecting variously the different levels of society, it should not be forgotten, as Carr-Saunders has pointed out, that "the reduction in the birth-rate may be that which economic conditions demand, and that it may of necessity have to begin with the upper classes." Though, therefore, he concludes, this differential fertility as lowering the average quality of the population is to be deplored, this may be less of a misfortune than if there were no reduction in the rate of increase, for without such a reduction economic requirements would not be satisfied.

On general evidence the inference is drawn that the decline in the birth-rate among those classes which show it is due largely

to deliberate volition in the regulation of the married state. Moreover, it is clear that in the interests of future generations control of some kind must be exercised more extensively, and eugenic considerations must not be neglected. The methods by which these results can best be achieved are a matter of dispute. Contraceptive practices in coition, although very widely used by all civilised peoples, and often without any deleterious results, are objected to by some authorities on the ground that they are liable to induce nervous or mental instability. Here we may be confronted with a choice between two evils, the risk of occasional neurasthenic disturbances on the one hand, and the disadvantages of undue propagation on the other, and it is probably right that here as elsewhere the immediate interests of the individual should be sacrificed to the general well-being of the community. Moreover, the effect upon the individual may often depend upon the particular practice adopted.

The employment of contraceptive methods is sometimes deprecated also on grounds of morality and religion, but this is a subject which is outside our present scope. It cannot be disputed, however, that in some way or other man must assume a more complete restraint over his reproductive functions and subordinate his inclinations to the future interests of humanity. It is only in regard to the manner in which this should be effected that there can be any serious difference of opinion.

Furthermore, it must be generally agreed that as the population problem becomes increasingly acute, it will be of advantage to the community that a greater flow of sexual energy should be "sublimated" (as Freud and his psycho-analytic school express it), that is, diverted into other and more profitable channels of an intellectual, social, or æsthetic order. That there are individuals who can successfully accomplish this has been implicitly recognised throughout all ages, for they number amongst them some of the greatest benefactors of mankind. It was something of this sort that Bacon meant when he wrote that "the best works, and of greatest merit to the public, have proceeded from unmarried or childless men, which, both in affection and means, have married and endowed the public," and Bacon did not refer merely to liberality and the endowing of worldly gain.

There is a good deal of confused thinking and writing about what is called "unnatural," and it is sometimes represented that

because a practice can be so described, therefore it is to be condemned as being ethically wrong. A very little consideration should be sufficient to convince one of the error of this view. We have only to remember the fundamental antagonism between the ethical process and the cosmic process, as Huxley called them—an antagonism which has been the theme of some of the world's greatest writers. Moreover, as Huxley observed, it is the duty of man to struggle constantly "to maintain and improve, in opposition to the state of Nature, the state of Art of an organised polity," and in order successfully to accomplish this it may be necessary for him to forego the right to multiply even as he has already foregone the right to murder or to steal.

The problem of population which Malthus first revealed is still far from being solved. For although Malthus obtained many adherents, and political economists have never quite lost sight of the essential truths which he expounded with such relentless logic, the great scientific discoveries of the Victorian period and their practical application, and the remarkable industrial development which consequently ensued, led to his views being neglected or discredited both by men of learning and by the public at large. It is improbable, however, that in a fuller world a period of industrial expansion like that of the nineteenth century can ever occur again, and in any case the available means of subsistence must eventually set a limit to man's increase upon the earth.

The problem is full of difficulty, but it has to be faced, even though it arouse acute social prejudices and involve serious international complications. Within a particular country it is sometimes regarded as a national question, and the raising of the birth-rate is enjoined as a duty in order that that country may take its proper place in the world. This view, if carried to its logical conclusion, can only lead to discord and disaster, as indeed it has already done in the past, and in our opinion a race for population between the nations is as deplorable as a race for armaments.

The solution of the difficulty is sometimes sought in emigration, but this, as Keynes says, "is only an expensive palliative. Indeed, the problem of population is going to be not merely an economist's problem, but in the near future the greatest of all

political questions. It will be a question which will arouse some of the deepest instincts and emotions of men, and feeling may run as passionately as in earlier struggles between religions. The issue is not yet joined. But when the instability of modern society forces it, a great transition in human history will have begun, with the endeavour by civilised man to assume conscious control in his own hands away from the blind instinct of mere predominant survival."

INDEX

[Names of authorities referred to are printed in small capitals; specific names in italic.]

A

B

C

H

I

J

K

L

M

N

O

P

T

U

V

PRINTED IN GREAT BRITAIN AT
THE DARIEN PRESS, EDINBURGH